ministry of
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A Wolverine Management Strategy for British Columbia

Wildlife Bulletin No. B-60
May 1989

BC
MINISTRY OF
ENVIRONMENT

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ISSN 0829-9560

A WOLVERINE MANAGEMENT STRATEGY FOR BRITISH COLUMBIA

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Prepared For:

B.C. Ministry of Environment
Wildlife Branch
Victoria, B.C.

Wildlife Bulletin No. B-60
January 1989

89-06176/

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Canadian Cataloguing in Publication Data

Hatler, David F. (David Francis)
A wolverine management strategy for British Columbia

(Wildlife bulletin, ISSN 0829-9560 ; no. B-60)

Includes bibliographical references.
ISBN 0-7726-0975-6

1. Wolverines - Control - British Columbia. I. British Columbia. Wildlife Branch. II. Title: III. Series: Wildlife bulletin (British Columbia. Wildlife Branch ; no. B-60)

QL737.C25H37 1989 639.9'7974447 C89-092184-9

The wolverine "...is simply an uncommonly large, clumsy, shaggy Marten or Weasel, of great strength, without corresponding agility, highly carnivorous, like the rest of its tribe, and displaying great perseverance and sagacity in procuring food in its northern residence when the supply is limited or precarious, often making long uninterrupted journeys, although so short-legged...it is a notorious thief; not only of stores of meat and fish laid up by the natives of the countries it inhabits, the baits of their traps, and the animals so caught, but also of articles of no possible service to itself; it avoids with most admirable cunning the various methods devised for its destruction in retaliation."

Elliott Coues, 1877

PART 1: SUMMARY

INTRODUCTION

Although relatively familiar to most trappers in British Columbia, the wolverine has been characterized as one of Canada's rarest mammals. As indicated in the opening quote, its relationship with humans and its reputation on this continent have developed primarily on the wilderness trapline, where it has often been considered more a competitor and nuisance than a resource.

However, it is now apparent that the myths and legends relating to the destructiveness of the "injun devil" have been over-dramatized, applying only to some individuals in some situations and not to the species as a whole. Rather, the sparsely occurring wolverine is a unique and is interesting animal, perhaps serving as an indicator of the health and productivity of local environments better than any other, and certainly standing as a challenge in resource use and management.

DISTRIBUTION

Historically, the North American wolverine is believed to have been present in most Canadian provinces, although it has probably never been abundant in the east. At present it is rare from the Prairies eastward, regularly occurring only in the extreme north in most of those provinces, and not at all in the Maritimes. However, the species continues to occur, as in historic times, in the north and west (Alaska, Yukon, NWT, and British Columbia), and expanding populations have been reported in recent decades in mountainous areas of Montana, Washington, and Oregon.

ASPECTS OF HARVEST

Because wolverines occur only in small numbers everywhere, their overall economic importance is not high. They rarely compose more than 2% of the total B.C. fur harvest value in any one year, even though B.C. is consistently the number one wolverine producer in Canada. Since the mid-1970's, the Canadian yield has averaged about 800 pelts, with B.C. contributing more than a third of those. Most B.C. harvests in recent years have been 200-300 animals, but a 3-year average in the mid-1970's was 550, with an all-time high of 634 in 1973-74.

Within the province, wolverines are apparently taken only rarely along the coast, especially in the south, and are protected on Vancouver Island, but they regularly appear in the fur harvest of all other regions. The highest and most consistent production is in mountainous

M.U.'s (management units) in the north (Omineca-Peace and Skeena Sub-regions), and in the southeast (Kootenay Region).

The provincial harvest is well dispersed, with most (about 80%) of successful M.U.'s producing 3 or fewer pelts in any one year, and with few (32%) producing 1 or more in all of the three most recent years. Among individual trappers who sold wolverine pelts in those years, most (about 90%) have had an annual yield of only 1 or 2.

HABITAT

Wolverines commonly occur above treeline, especially in summer. Spruce and fir forests are often used for resting and foraging cover in winter, and in that season at least some individuals are known to descend to lowlands along rivers and lakes, associated with wintering ungulates. High elevation conifer forests appear to be a regular feature of wolverine habitat in most areas, although one studied population in northwestern Alaska existed year-round on the open tundra.

Snow is an important component of the wolverine's seasonal habitat, providing a deep insulative layer over the den where the young are born in late winter, and often negatively affecting other wildlife, especially ungulates, so that they become available as carrion from predation or winter-kill.

LIFE HISTORY AND POPULATION DYNAMICS

Food and Nutrition

The wolverine has been called "the hyena of the north" because of its basically scavenging lifestyle. However, it procures much of its own food in summer, including the eggs and young of ground-nesting birds, various mice, voles, and berries, and it may focus particularly on burrowing rodents (marmots and/or ground squirrels) in most areas.

In winter, ungulates such as moose, caribou, and elk form an important part of the diet. The wolverine's reproductive schedule, with the young born in February or March, appears to be timed to coincide with the period of maximum availability of ungulates, which are mostly taken as carrion from animals dying of starvation or from predation by larger carnivores such as wolves and cougars.

Extreme hunger seems to be a regular feature of wolverine existence, and individuals may survive for long periods on the most meager diet, actually digesting and deriving some nourishment from bone and scraps of hide. However, females are apparently unable to raise young under such circumstances. In general, the most severe winters in terms of ungulate survival may be the best years for the well-being and productivity of wolverines.

Home Range and Territoriality

Despite their reputation as travelers, radio-tracking has shown that individual adult wolverines establish and largely confine their activities within distinct home ranges. Those ranges may be 600 km^2 or larger in area, although only a portion of that total area may be used in any one season.

Adults appear to maintain their home ranges more or less separate, by territorial behavior, from those belonging to adjacent animals of the same sex. The ranges of adult males are the largest, and may contain the ranges of up to 4-6 females, especially in summer (mostly late May through July) when breeding occurs.

Activity and Movements

Unlike many other carnivores, wolverines are commonly active during daylight hours. Daily movements of 20-30 km or more are known, but there is evidence that the nature and extent of movements, especially in winter, may be related to nutrition. An animal that has located a concentrated food source such as a large ungulate carcass may remain at that site, with little movement, for up to 3-4 weeks, while an individual having difficulty finding food may travel beyond the boundaries of its usual area of activity.

The longest recorded movements, up to 378 km, represent dispersal of young animals that have not yet established home ranges. Dispersal is important as a source of replacement and recolonization, particularly where local numbers are depressed and/or productivity is inadequate.

Reproduction

Wolverines have a relatively low reproductive potential. The earliest breeding among young females is in their second year, but many at that age may not produce young. Adults may also fail to produce young in some years. Up to 6 embryos have been found in pregnant females, but no live litters larger than 4 have been reported and most are in the range of 1-3. There is evidence that late winter nutrition may be a major factor in individual productivity, with inadequate food resulting in failure of females to complete pregnancies, poor early survival of kits, or both.

Health and Mortality

Wolverines support a variety of parasites, including a species of tapeworm that they get from eating porcupines. However, no chronic parasite or disease problem affecting populations has been identified. It appears that the level of nutrition may be the factor most consistently affecting the condition of individuals.

The most common sources of mortality among radio-collared animals have been harvest by humans and starvation. In addition, there have been a number of reports of wolverines being killed or injured in attacks by other species, especially wolves. Thus, wolverines appear to be both dependent upon other carnivores for a portion of their winter food supply, and in danger from them as predators/competitors.

Numbers and Composition

Wolverine populations are composed of animals with established home ranges (residents), and those without (transients). The transients are mostly dispersing young, but may also include older animals that have abandoned home ranges because of injury, infirmity, and/or inadequate food supplies. It is believed that because male ranges are larger than those of females, there are fewer available and males therefore remain longer and are most common among the transient class.

In general, transients are less secure than residents, traveling more and often in unfamiliar terrain. They may therefore be more regularly exposed to extreme hunger problems, and are generally the most likely to encounter trap sets and/or to come into conflict with man. Females with young have high nutritional demands, but appear to be less mobile than other classes, especially during the early weeks after giving birth.

The most intensive field studies have produced minimum local density estimates of 1 wolverine per 50 km^2 to about 1 per 200 km^2.

However, those studies have generally been unable to adequately account for transients, which may be particularly important both in the harvest and in population maintenance.

POPULATION MANAGEMENT

Vulnerability to Trapping

Those who have studied wolverines by following tracks in winter, report the impression that the animal is simply "looking for something to eat" rather than truly hunting. It often follows the tracks of other carnivores such as wolves, foxes, and lynx, and regularly uses food items cached or left by those species.

Thus, it is likely that encounters with humans result from similar behavior, with the animals treating human caches and trap sets as they would other potential food sources along the trail. Although that would suggest that they are particularly vulnerable to trapping, there is evidence that they are also naturally wary and quick to learn. In short, it appears that wolverines are not all equally trappable, and that both experience and condition may play a role in the differences between individuals.

Data presently available indicate that males and young animals tend to predominate in the harvest, particularly in the early months of the trapping season. That result is consistent with the view that the least secure animals nutritionally-- usually juveniles and/or transients before adults and/or residents--are the most vulnerable to trapping. The vulnerability of adults probably increases with advanced age and with the progressing winter, the latter more in some years than others and particularly for females with developing young.

Harvest Management

Because present harvests in British Columbia are well dispersed, i.e., with few coming from any one area, there seems little opportunity to manage harvest levels with bag limits or quotas. Focussing the harvest on the least secure segment of the population would appear to be a sound management strategy, and that is probably best accomplished by manipulation of season closure dates to protect the most secure and productive members of the population. Although more and better harvest data are required, it appears that present season dates in B.C. are adequate at existing harvest levels.

Maintenance of refuge areas to produce dispersing animals both for harvesting and recruitment is also required. That can be at least partly accomplished voluntarily by trappers. The need is to avoid trapping intensively for wolverines in all portions of each trapline.

Population Monitoring

Census of wolverines over large areas would be impractical, and is unlikely to become a regular feature of management. In the foreseeable future, the only significant source of information about wolverine populations in the province will likely be trappers, thus it is important that they cooperate in providing reliable harvest data and specimen material, and conscientious replies to various questionnaires.

It is recommended that the skulls of wolverines be collected routinely, to provide continuing information on the sex and age composition of the harvest in various areas under varying conditions.

HABITAT MANAGEMENT

No particular habitat components or habitat management techniques can presently be singled out specifically for wolverines. As yet undescribed "refugia" appear to be of major importance, and the success of the wolverine in B.C. to date may relate to the availability of large areas of remote, rugged uplands that are difficult of access to humans, and which have rarely been subject to competing land uses.

Overall, it seems apparent that the presence and viability of wolverine populations relates to the viability of the entire local ecosystem. Thus, a broadly focussed, integrated approach that promotes and protects biological diversity and richness is required.

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PART 2: THE BIOLOGY AND MANAGEMENT OF WOLVERINE

2.1 INTRODUCTION

This section provides a narrative summary of the biological and social factors that seem most clearly to relate to the subject of a wolverine management strategy for British Columbia. It is primarily a literature review, based on the 180 references listed and described in the annotated bibliography (Part 3), and is parallel in most respects to the previous document in this series, dealing with lynx[1]. Although wolverine and lynx are very different morphologically and ecologically, it develops that they share a number of common features, particularly in terms of zoogeographic history and origins, Holarctic taxonomic relationships, North American distribution patterns, and their present management status in B.C. Throughout this report, occasional references are made to similarities and differences between the two species that seem relevant. In every case, references to lynx findings are from the management strategy report footnoted below, and no additional documentation is given.

As in the comparable section of the lynx report, the operative term here is MANAGEMENT--the collective actions both by trappers and by professional wildlife and habitat managers, to sustain and/or enhance populations of the species. Other recent reviews, particularly Wilson (1982) and Hash (1987), have provided detailed coverage of wolverine descriptive features and biology, therefore a similarly directed effort is not presently required. The general approach in this review is to proceed systematically through a list of subject headings and keywords generated in the bibliography (Part 3), and to briefly discuss each in terms of its known or potential relevance to management. To provide an overall perspective, initial sections characterize the body of literature available and describe the history and status of wolverine management and research in British Columbia.

2.1.1 Characteristics of Literature on Wolverine

The subject index lists the frequency of occurrence of various subject headings and keywords used to describe and categorize the references identified in the bibliography (Part 3). Compilation of those frequency data enables the following generalizations about the body of wolverine literature that has been assembled:

Geography - Only a relatively small proportion of the 180 references listed in Part 3 related to general locations such as the species Holarctic distribution (1.1%), North America (2.7%), or Canada (3.8%). Within Canada, the provinces and territories that were the subject area for the most papers were British Columbia (14.2%), Northwest Territories (5.5%), Alberta (3.8%), and Yukon Territory (2.2%). As will become clear, the high proportion of B.C. papers reflects selectivity and less rigid rejection criteria rather than an abundance of pertinent information. The other five Canadian jurisdictions listed were each featured in 1.1% or less of the assembled papers.

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[1]Hatler, D.F. 1988. A lynx management strategy for British Columbia. Rep., B.C. Ministry of Environment and Parks, Victoria. 127pp.

The most frequent specific source location outside of Canada was Alaska (13.7%), while only two other states, California (4.9%) and Montana (4.4%), appeared in 3% or more of the papers. A total of 23 papers (12.6%) were set in Eurasia, especially the Scandinavian countries.

Methods - Among 175 papers for which methods could be tabulated, the largest proportion (42.7%) were indoor (paper) projects, mostly reviews and syntheses of both published and anecdotal information. Indoor projects of a more truly biological nature (20.0%) involved various laboratory studies, including autopsy and analysis of harvest samples, food habits analyses, study of museum specimens, and experiments with captive animals. Although over a third of the papers reported results from outdoors (37.7%), the great majority of those were based on one-time incidental observations (29.1%). Methods used in actual field studies included telemetry (2.9%), snow-tracking (3.4%), and combinations of those and other methods (1.1%). Although the above general pattern for distribution of study methods is similar to that recorded for lynx, the number and proportion of intensive field and laboratory studies are considerably smaller for wolverine than for lynx.

Management Significance - Of 175 papers subjectively rated as nil, low, medium, or high in terms of their perceived significance to management, only 7 (4.0%) were judged high and 20 (11.4%) were considered medium. Those in the high category include six North American studies, all conducted within the past two decades, that managers should be particularly aware of. Listed chronologically, they include a multi-faceted laboratory study of a large series of specimens from Alaska and the Yukon (Rausch and Pearson 1972), a pioneering field study, including use of telemetry, in Montana (Hornocker and Hash 1981), and recent intensive field studies, with telemetry, in southcentral (Gardiner 1985) and northwestern Alaska (Magoun 1985, 1987), and in the Yukon Territory (Banci 1987). Four papers in the "medium significance" group, so rated because they are somewhat out of date, should also be highlighted here as the best syntheses on Canada-wide wolverine status and management needs. They are Dagg and Campbell (1974b), Van Zyll de Jong (1975), Holbrow (1976), and Kelsall (1981). The Holbrow paper is also the primary source for information on the considerable body of "legend and mythology" associated with the wolverine. It seems significant to note that of the ten papers listed above, only four (Rausch and Pearson 1972; Van Zyll de Jong 1975; Hornocker and Hash 1981; Magoun 1987) are available in easily accessible biological sources. The others are graduate theses (4) or unpublished reports (2).

Topics - Among 175 indexed papers, the most frequently occurring subject headings were Description (53%) and Life History (51%), while Population Dynamics and Species Management followed at 33% and 26%, respectively. Most of the papers under Description (all but 5%) were categorized under distribution, and were simple reports of occurrence. The species is sufficiently rare in most areas so that its mere appearance has frequently been considered of publishable importance. The Life History topic featured most often (26%) was behavior, mostly accounts of depredations on traplines or at human cabins and caches in remote areas. The only other topics in that category that were covered in 10% or more of the papers were food studies (16%) and considerations of health (parasites, disease, condition, 10%). Most of the papers under Population Dynamics were in the category "poptrend", and were usually little more than subjective estimates of population status, while the most frequently appearing item under Species Management referred to some aspect of the harvest (9%). As with lynx, Habitat and Habitat Management were the least addressed topics, with only 5% of the papers describing specific cover types used by wolverines and less than 2% offering or implying habitat management recommendations.

2.1.2 Wolverine Management/Research In British Columbia: A Review

Although 26 of the references located (14.2%) featured B.C. as the primary geographical location, all but a few of those mentioned wolverine only as one of several mammals covered. Those most sharply focussed on the species in B.C. include a brief taxonomic review based on two specimens from Vancouver Island (Goldman 1935), an account of an unsuccessful wolverine attack on mountain goats (Guiguet 1951), a report on some early reconnaissance field work on traplines in the Fort Nelson area (Quick 1953b), an unpublished report on snow-tracking observations in Mt. Assiniboine Provincial Park (Cockerton and Herrero 1973), an account of age and reproductive characteristics of a small sample of trapped animals from northwestern B.C. (Liskop *et al.* 1981), a status review focussing on the Vancouver Island form (Banci 1982b), and a report on field experiments involving the use of wolverine odors to repel snowshoe hares from eating conifer seedlings (Sullivan 1986). In addition, aspects of provincial distribution and abundance of furbearers, including wolverine, have occasionally been inferred from harvest data (e.g. Cowan 1936; Bandy 1952; Edwards and Cowan 1957). Harvest data and a series of interviews of both managers and trappers were used by Holbrow (1976) in his analysis of wolverine trapping characteristics, image, and population status in the western provinces, including B.C. There have been no detailed field studies in the province, although the recent work by Banci (1987) in southwestern Yukon is near the B.C. border in that area.

The most recent management statement for the wolverine in British Columbia, as one of several mustelids in the province, is that by Munro and Jackson (1979). As outlined in that document, the guiding policy for the furbearers listed is that they "...will be managed primarily for commercial use as fur-bearing species" and that "Humane trapping methods will be promoted. The stated management objectives are to:

1) "Maintain...present diversity, range, and population levels.."

2) "Manage...in response to harvest demands."

In addition, the following "management prescriptions" are specified or implied as being directed to wolverines:

1) "Protect critical habitat..." (which) "...consists of mature conifer stands..."

2) "Establish inventories to obtain population indices..."

3) "Set harvest levels and seasons in accordance with known population characteristics.

4) "Monitor harvests to indicate...population status."

5) "Encourage trappers to engage in education programmes in humane trapping techniques and in resource planning to ensure protection of the mustelid family."

Lack of inventory data, habitat destruction, and inadequate knowledge of habitat requirements are identified as the major problems in mustelid management in the province.

2.2 DESCRIPTION

2.2.1 Features

Local differences in form or size might suggest local biological differences that should be taken into account in management. A comparison of weights from several areas (Table 1), indicates that wolverines are similar in size throughout their Holarctic range. The greatest differences are between the sexes, with males averaging larger by about 30-40% (13-14 kg vs. 9-10 kg).

As with lynx, and perhaps to an even greater degree, physical uniformity within the species may result from the species mobility, with low population density and wide-ranging dispersals combining to provide little opportunity for local segregation of gene pools. There is some justification, therefore, for assuming that wolverine study results from other areas are applicable to management deliberations in British Columbia.

2.2.2 Taxonomy

As with lynx, the Old World and New World forms of the wolverine were formerly considered to be separate, but are now lumped together as the only two subspecies of one circumpolar species. The applicable names are *Gulo gulo gulo* for the subspecies in Eurasia and *G. g. luscus* for that in North America (Kurten and Rausch 1959). Those authors hypothesized that *luscus*, which differs little from fossil material on either continent, is a relatively recent immigrant, perhaps arriving in North America during one of the later stages of the Pleistocene. Based on only two specimens, Goldman (1935) listed the Vancouver Island wolverine as a distinct subspecies (*vancouverensis*). However, the validity of that status was doubted by Cowan (1936) and has recently been rejected by Banci (1982b). Thus, consistent with the above conclusions relating to size, the North American wolverine appears also to be monotypic in form, such that managers are dealing with the same animal wherever on this continent it may occur.

2.2.3 Distribution

The present range of the wolverine in North America, as depicted in numerous publications (e.g., Wilson 1982; Hash 1987) is essentially the northern forest and tundra, with southward extensions in the western mountains. The species is believed to have occurred historically in most continental (non-island) Canadian provinces, although possibly less abundantly in the east. It was apparently extinct in New Brunswick by 1850, and its range has shrunk to the extreme north in Quebec, Ontario, and the prairie provinces, but there has been no known change from the pristine distribution in British Columbia or the Territories (Dagg and Campbell 1974b; Van Zyll de Jong 1975).

Table 1. Some weights of wolverine (kg) in Eurasia and North America. All specimens were believed subadult (age 2) or older, unless footnotes indicate otherwise

Location (Sample[1])	Male			Female			Source[2]
	N	Mean	Range	N	Mean	Range	
EURASIA							
USSR[3]	9	14.0	12.5-17.0	5	9.9	9.0-10.4	1
Norway (NS)[3]	51	14.6	-	39	9.9	-	2
Finland (NS)[3]	-	-	-	20	11.0	-	2
NORTH AMERICA							
Alaska (WW)	6	14.5	13.2-16.8	2	9.8	9.5-10.0	2
Alaska (PW)	61	12.9	9.3-19.3	50	8.8	6.8-10.5	2
NW Alaska (LW)	7	14.1	12.5-15.9	12	9.9	9.5-10.9	3
S-Central Alaska (LW)[3]	10	15.8	14.1-17.7	2	10.0	9.5-10.5	4
Yukon (WW)	52	14.2	11.9-16.5	21	9.4	8.3-10.8	2
Yukon (LW)[3]	5	13.0	10.2-15.0	5	8.7	6.6-11.0	5
Yukon (PW)	155	12.5	-21.3	112	8.5	-14.4	5
NW B.C. (PW)	41	12.8	9.4-18.6	35	8.8	5.8-13.8	6
Vancouver Isl. (WW)	-	-	-	2	7.8	6.7- 8.8	7
N-Central B.C. (WW)	1	12.7	-	-	-	-	8
Alberta (WW)	-	-	-	1	8.8	-	9
Montana (LW)[3]	7	12.4	10.8-14.5	10	7.9	6.4- 9.5	10
Washington	2	13.0	12.7-13.2	-	-	-	11
Idaho	1	10.0	-	-	-	-	12
Iowa	-	-	-	1	10.0	-	13
Oregon	1	12.7	-	-	-	-	14

[1] Nature of sample: LW = live weights of captured animals; WW = whole weights of dead animals; PW = projected weights of skinned carcasses (25% added, as suggested by Rausch and Pearson 1972); NS = not specified.

[2] Sources: 1) Makridin 1964, 2) Rausch & Pearson 1972, 3) Magoun 1985, 4) Gardiner 1985, 5) Banci 1987, 6) D. Nagorsen, Royal B.C. Museum files (data from Liskop *et al.* studies), 7) Cowan & Guiguet 1965, 8) D. Hatler (unpubl. data, Bulkley Valley area, B.C.), 9) Scotter 1964, 10) Hash and Hornocker 1980, 11) Patterson and Bowhay 1968, 12) Pengelley 1951, 13) Haugen 1961, 14) Kebbe 1966.

[3] Sample known or suspected to include young-of-the-year.

As was the case for lynx, many of the papers indexed in the bibliography under "distribution" are accounts of rare appearances outside the usual range, e.g. in a deciduous forest in southern Quebec (Miller 1972), on the prairie of southern Alberta (Scotter 1964), and in an Iowa cornfield (Haugen 1961). However, most observations in the contiguous 48 states in recent decades have been in the west, particularly in and around the Rockies and Cascade Mountains. After near absence from those areas through about the first half of this century, the species first reappeared and increased to viable numbers in northwestern Montana (Newby and Wright 1955, Newby and McDougal 1964). Increases in sightings were also documented farther west, in Idaho, Washington, Oregon, and northern California (Pengelley 1951; Yocum 1973, 1974). For most of the above range expansions, dispersal from Canada (i.e., British Columbia) is credited as a major source of the initial colonizers.

The range within British Columbia has not been precisely defined, but is listed as "...throughout the province in the mountainous areas..." by Cowan and Guiguet (1965). Those authors, and Liskop *et al.* (1981) indicated that the species may be uncommon along the coast, especially in the Lower Mainland area. However, the species' only known island occurrences south of the arctic (where ice crossings are possible), are in the west, e.g., Wrangell Island in southeastern Alaska (Webster 1949) and Vancouver Island (Banci 1982b), and records from the British Columbia Royal Museum indicate specimen locations such as Stewart and Prince Rupert (File notes, courtesy D. Nagorsen, pers. comm.). Given the rich scavenging opportunities along the B.C. coast, particularly in the form of spawned-out salmon which are known to attract concentrated use by wolverines elsewhere (Banci 1987), it seems likely that the hypothesized coastal rarity actually reflects the local sparsity of human observers in that area. Records for the past 3 years (Section 2.6.2), indicate wolverines harvests in all Administrative Regions except the Lower Mainland and Vancouver Island, with the bulk coming from the north (Skeena and Omineca-Peace) and from the Kootenay Region.

2.3 HABITAT CHARACTERISTICS

The general habitat of the European wolverine is given as "forest and tundra" (Erlinge 1986), "...in low mountains or...coniferous forest bordering on the high mountains" (Haglund 1966), and "...swamp areas of the northern coniferous forest region" (Krott 1960). The species is also identified with the northern coniferous forest in North America, occurring in climax and various subclimax associations throughout that "biome" (Shelford and Olson 1935). Wilson (1982) stated that wolverines are "...particularly fond of marshy areas", and that they are limited to montane habitats in the southern parts of their range.

Quick (1953b) believed that northwestern British Columbia, in the vicinity of Fort Nelson, constituted a "center of wolverine population in western Canada", and noted that the species occurred in about equal densities in all of the three physiographic subdivisions of the local "Taiga Biome" (muskeg, foothill, and mountain). However, on the basis of harvest distribution in B.C. boreal forest over a 20-year period, Edwards and Cowan (1957) found that the highest production was on the "high, cold plateaux in the northwest" (Yukon Forest), with somewhat lower production in the Liard Forest, and with the lowest production in the eastern lowlands (Nelson Forest).

Further, even within the area of generally lowest yields in the northeast, there was a west-to-east cline with the highest production near the mountains. In an area of southeastern B.C. (Kootenay National Park), the wolverine's primary habitat was listed as the "sub-alpine forest biotic area" (Munro and Cowan 1944). and for the province generally the species is described as "...a creature of the northern wilderness, frequenting wooded and mountainous areas" (Cowan and Guiguet 1965).

North American wolverines have been intensively studied in the arctic tundra of northwestern Alaska (Magoun 1985), in sparsely forested mountain habitats in southcentral Alaska (Gardner 1985) and southwestern Yukon Territory (Banci 1987), and in a diversely forested wilderness area in northwestern Montana (Hornocker and Hash 1981). The detailed descriptions of those study areas are important in their demonstration of the range of habitats that may support viable wolverine populations, but they have little direct management utility and will not be discussed further.

2.3.1 Cover

As used here, the term "cover" refers to the particular portions of study areas or other described habitats that are actually used by wolverines. In the three telemetry studies cited above where a local choice of habitats existed, attempts were made to document selection by the species, with the following results:

- Northwestern Montana, based on 576 radio-locations (70% female) from up to 24 animals, and some snow-tracking (Hornocker and Hash 1981):

  Most relocations (70%) were in medium or scattered mature timber, with a strong selection for forests featuring alpine fir, while the rest were primarily in ecotonal areas. Dense young timber, burns and wet meadows were rarely used, and there were no relocations in logging clearcuts. Snow-tracking showed that the animals occasionally crossed clearcuts, but usually in a straight line and at a running gait, as compared to more leisurely and meandering (hunting) patterns in the timber. Bed sites were often in snow on open outcrops, but "...all in timber types which afforded cover." A distinct seasonal elevational pattern was documented, with the wolverines occupying higher ranges during the snow-free season than in winter.

- Southcentral Alaska, 178 radio-locations (mostly males), and some snow-tracking (Gardner 1985; Whitman *et al.* 1986):

  Spruce communities and ecotonal areas, especially rock outcrops, were used significantly more than expected in relation to availability. On a seasonal basis, forest types (spruce, mixed, and deciduous) were avoided and other types (shrub, alpine tundra, rock/ice) were used according to their availability in summer, while tundra was avoided and the others used according to availability in winter. Winter snow-tracking showed that the animals hunted primarily in spruce types in that season, and usually made only straight-line

movements through shrub and deciduous types. Seasonal differences in elevation were documented, with the animals using selecting upland types in summer and moving to adjacent lowlands for winter.

- Southwestern Yukon, 151 radio-locations (67% female) for 5 animals, and some snow-tracking (Banci 1987):

  Different patterns were documented for different individuals, but habitat use by females did not differ from availability either generally or seasonally, while the males used subalpine conifer habitats more in winter and alpine talus less in summer than expected based on availability. Two of the five animals, an adult male and an adult (denning) female showed a seasonal shift in elevation, but the other three animals did not. There appeared to be some selection for sparse habitats in winter and against closed canopy habitats in summer, and no reluctance to cross large natural openings was noted.

Some consistent patterns are evident, particularly the species' general affinity for high latitude and high elevation (and associated tree-line forests of spruce and fir), and the tendency for seasonal vertical migrations in mountain areas. However, there is as yet no evidence that wolverines are dependent upon any particular cover type. Munro and Jackson (1979) speculated that mature conifer stands constitute "critical habitat" for the species in British Columbia, but the observations of Magoun (1985) involved a population of wolverines that subsist year-round north of the arctic treeline, i.e., with no forest cover of any kind. Commenting on the effects of wildfire on wolverines, both Bailey (1981) and Stephenson (1984) concluded that there is no apparent detrimental effect of forest loss in the short term, and that post-fire successional increases in food species (moose, hare, beaver) will constitute a benefit to the species in the long term.

Although forest cover may be of particular significance to wolverines in some areas by providing escape from wolves (see Section 2.5.3), most observed patterns of seasonal movements and habitat use appear to have a nutritional basis. For example, the elevational migration pattern in southcentral Alaska is believed explainable by the animals focussing on an abundant supply of ground squirrels, other small mammals, and ground nesting birds in upland areas in summer, and then moving to lowlands where local ungulates winter and become available as carrion via wolf kills and starvation. Likewise, Banci (1987) believed that the higher than expected winter use of subalpine conifers by two of her instrumented animals was due to the presence of ungulate kills in those areas. She emphasized that habitat use by individual wolverines will vary with local differences in the distribution and availability of food resources, and concurred with Kelsall (1981) that "Habitat is probably best defined in terms of adequate year-round food supplies in large, sparsely inhabited wilderness areas, rather than in terms of particular types of topography or plant association."

2.3.2 Climate

Climate is a conspicuous feature of habitat in its influence on vegetation characteristics, but weather factors may also act directly on animals and may influence our view of population status,

for example through effects on trapper success. For the wolverine, it is apparent that one of the most important features of the environment is snow, and the species' annual cycle generally reduces to two "seasons", winter and summer, as defined by presence or absence of snow cover. The same might be said for most northern mammals, but in the case of the wolverine it appears to be the period of snow cover that is the more favorable. The species is well adapted for snow, with pelage renowned for its frost and cold repelling qualities (Hardy 1948; Quick 1952), and with a weight-loading that gives it a mobility advantage over many other species in deep or soft snow (Krott 1960; Gill 1978).

In the arctic study area of Magoun (1985), where a wind chill factor lower than -31° C occurs more than 50% of the time between December and February, wolverines apparently engage in considerable subnivean activity, creating systems of snow caves and tunnels extending 30 m or more. It is in such snow caves, and mostly in late winter when snowpack is thickest, that the young are born (Pulliainen 1968; Rausch and Pearson 1972; Magoun 1985). The importance of the snow cover as insulation for the young has been discussed (Pulliainen 1968), but most accounts suggest that the primary reason for that particular reproductive schedule is nutritional (see discussion in Banci 1987). In particular, wolf and winter-killed ungulates are available as carrion, and live ungulates are often in their most weakened and vulnerable condition of the year at that time. Of particular interest is the possibility of an inverse relationship between wolverine well-being/productivity and winter severity--as noted by Banci (1987), "higher than average survival of ungulates in winter will result in fewer carcasses for scavenging by wolverine" (and) "these times of low food availability...will be times of curtailment of reproduction."

The foregoing preview is only to establish perspective on the relationship of climate factors to wolverine ecology, and more details on most of the above topics are provided in later sections. It is acknowledged that weather conditions are not directly subject to management, but their effect on aspects of population dynamics and/or harvest vulnerability must be understood in order for management to be either responsive or predictive.

2.4 LIFE HISTORY

As in the lynx review, the distinction between life history and population dynamics topics is subjective. In general, the life history category includes those aspects of biology that can be thought of in terms of the single animal or, as in the case of food habits, the input from series of single animals, while population dynamics topics are those directly relating to numbers of animals. All life history topics discussed below are perceived to have management implications, i.e., can affect populations, although their effects are usually a step or more removed. Social behavior may be more directly related to abundance than many of the other topics listed, but it is nevertheless included under life history because it is expressed at the individual level. Mortality and natality both act at the individual level, and could therefore be considered under life history by that criterion, although their role in population dynamics seems obvious enough to include them there.

2.4.1 Food

Table 2 summarizes the major foods of the North American wolverine, as identified in the few detailed studies to date. Specifically, it lists those items that ranked in the top three, by frequency and/or volume, in each of the reported study samples. However, Banci (1987) has emphasized the uncertainty and unpredictability of food sources for the species (perhaps particularly in winter), and was of the opinion that "it is misleading to identify only one prey group as being the most important..." Accordingly, Table 3 lists all of the items for which I found reference to actual or intended use as food by wolverines on this continent. Both tables suggest that, on a continuum from food generalist to food specialist, the wolverine is on the opposite end from the hare-dependent lynx. In a large winter sample of digestive tracts from the Yukon, Banci (1987) identified remains of all 6 available species of wild ungulate and 11 species of rodents, including 5 of 6 available sciurids and at least 4 microtines.

The general pattern in the North American studies, however, is essentially the same as that described for the Old World form, with ungulates featured in the winter diet and becoming increasingly important as winter progresses, and with smaller items such as rodents, birds and eggs, and berries predominating in summer (Haglund 1966; Krott 1960; Myhre and Myrberget 1975). Although wolverines occasionally kill ungulates that are in a weakened state and/or rendered at a disadvantage by snow conditions, all authorities seem to agree that the animals obtain most of their ungulate meals by scavenging. Indeed, most general accounts of the wolverine highlight its morphological and behavioral adaptations for "a scavenging lifestyle", with one (Ewer 1973) referring to the animal as "the hyena of the north".

Snowshoe hares ranked second by frequency of occurrence in general samples from Alaska (Rausch and Pearson 1972) and the Yukon (Banci 1987). It had been speculated earlier (Cowan 1938) that wolverines might consume large numbers of that species during peak hare years, but the Yukon results were from samples collected during and after the hares' cyclic decline. Since snow-tracking observations have not shown wolverines hunting by stealth or strategy (Haglund 1966; Hornocker and Hash 1981; Gardner 1985), it seems likely that hares are also taken primarily by scavenging (defined in a broad sense to mean use of foods captured and then left or cached by other species).

It is nevertheless clear that wolverines do systematically seek and capture some prey species, particularly microtine rodents and certain sciurids. Ground squirrels and marmots are the most frequently appearing items in Table 3, and accounts of wolverines digging for them in habitats ranging from arctic tundra in Alaska (Magoun 1985) to the mountains of California (Fry 1923; Ruth 1954) suggests that along with the "hyena" image, an epithet of "tundra badger" might also apply. On this topic, one wonders about the relationship between the fully protected Vancouver Island wolverine and the unique, and endangered Vancouver Island marmot.

Table 2. Major foods of wolverine in North America, as recorded in the literature

		Rank and % Occurrence of Prey Items (Sp.[1])									
		No. 1			No. 2			No. 3			
Location	Samp.[2]	Sp.	Freq.	Vol.	Sp.	Freq.	Vol.	Sp.	Freq.	Vol.	Lit[3]
Alaska	D-W-20	CU	60	-	PP	15	-	-	-	-	1
Alaska	D-S-1	GS	100	-	MV	100	-	-	-	-	1
Alaska	D-W-94	CM	29	-	SH	24	-	CC	18	-	2
Yukon	D-S-1	BB	100	-	-	-	-	-	-	-	2
NW Alaska	0-S-48	GS	40	-	CC	13	-	MV	13	-	3
NW Alaska	S-W-82	GS	40	32	CC	37	35	MV	30	6	3
S. Alaska	D-W-35	CM	25	41	CC	20	20	MV	20	7	4
Yukon	D-W-316	CU	33	31	SH	19	7	CM	10	13	5
Montana	S-W-56	CD	45	-	CU	27	-	SH	17	-	6

[1] Sp. (Prey species and/or groups) - BB = blueberries; CD = carrion (domestic cow and/or horse); CC = carrion (caribou); CM = carrion (moose); CU = carrion (unident. wild ungulate); GS = ground squirrel; MV = mice and/or voles (Cricetidae); PP = porcupine; SH = Snowshoe Hare.

[2] Samp. (Characteristics of the sample) - 3 items representing:
- Type (S = scats, D = digestive tracts, O = direct observations.
- Season (W = winter--November-April, S = "summer"--May-October,
- Sample size.

[3] Lit (Literature Source): 1) Rausch 1959; 2) Rausch and Pearson 1972; 3) Magoun 1987; 4) Gardiner 1985; 5) Banci 1987; 6) Hornocker and Hash 1981.

Table 3. Range of seasonal[1] food items used by wolverines in North America, as reported in the literature

FOOD ITEMS[2]	SOURCES[3]																
	Alaska							Yukon		NWT		BC	Lower 48				
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
UNGULATES																	
Moose		W	B					W		W							
Caribou		W	W	B		W		W									
Elk								W							W	W	
Deer*								W							W		
Thinhorn Sheep								W		W							
Mountain Goat								W				S					
Cow/Horse														S	W		
Unident.	W		W					W									
RODENTS																	
Porcupine	W	N	W					W							W		
Beaver		W	B					W							W		
Marmot*		S		S				W	S				S		W		S
Ground Squirrel*	S	S	B	B	S			B					S		S		S
Red Squirrel			W					W									
Flying Squirrel								W									
Chipmunk*								W									
Voles/Mice	B	B	B	B	S			W					S		W		
OTHER MAMMALS																	
Snowshoe Hare	W	W						W							W		
Pika								W									
Shrews*				W				W									
Wolverine			W														
Marten								W									
Mink								W									
Weasel*								W									
Red Fox				W													
Coyote								W									
Wolf								W									
Lynx		W						W									
Whales*		N															
Pinnipeds*		N															

Table 3, continued

FOOD ITEMS[2]	SOURCES[3]																
	Alaska							Yukon		NWT		BC	Lower 48				
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
BIRDS																	
Ptarmigan*			W	B				W	W								
Gull*								W									
Corvid*	W							W									
Raptor*	W		W					W									
Duck*				W			S										
Unident.	W	W	B					W							W		
Eggs				B										S			
OTHER																	
Fish*	W	W						W									
Insect*								W									
Berries*		S						W									
Garbage								S									

[1] Season of use is indicated in the body of the table by W (winter, about November through April), S (summer, May through October), B (both winter and summer), or N (season not specified).

[2] Items indicated are all species described or implied to have been eaten, cached, or pursued; those with asterisks indicate known or suspected incidences of one or more species in the group indicated; consult original sources for scientific (Latin) names.

[3] Source: *Alaska* - A) Rausch (1959); B) Rausch and Pearson (1972); C) Gardner (1985); D) Magoun (1985, 1987); E) Bee and Hall (1956); F) Burkholder (1962); G) Webster (1949).
Yukon Territory - H) Banci (1987); I) Youngman (1975).
Northwest Territories - J) Boles (1977); K) Gill (1978).
British Columbia - L) Guiguet (1951).
Lower 48 States (U.S.A.) - M) Fry (1923); N) Haugen (1961); O) Hornocker and Hash (1981); P) Houston (1978b); Q) Ruth (1954).

It seems significant that both ground squirrels and marmots, though hibernators, were identified in all of the winter wolverine food samples cited in Table 2. In arctic Alaska, ground squirrels dug up from caches and/or from hibernacula were as conspicuous and possibly as important in the winter diet as caribou, the only available ungulate (Table 2).

Red squirrels appeared with fair frequency in winter food samples both in the Yukon (Banci 1987) and in southcentral Alaska (Gardner 1985), and the latter author reported evidence of wolverines digging at squirrel middens. Since wolverines frequently hunt by day, the potential for encountering the day- active squirrels on the ground and/or trapping them in the tunnels and burrows associated with middens would seem to be good, especially where the squirrels are abundant. Porcupines are used in most areas, but long retention of quills apparently makes it difficult to evaluate the importance of that prey species (Banci 1987). I trailed a wolverine about 2 km in Glacier National Park, B.C., and a fresh scat deposited by that animal was 100% porcupine hair and quills, mostly the latter (D. Hatler, personal notes).

Although above paragraphs describe aspects of the species' diet, they do not transmit a sense of the extreme circumstances to which individual animals may be exposed during the season of scavenging. The accounts from northwestern Alaska (Magoun 1985, 1987) do that particularly well, since the main winter foods available there are cached and/or hibernating ground squirrels and the remains of caribou that died before fall migration. The use of cached ground squirrels involved gnawing the animals out of the frozen ground, with the result that soil was often a frequent and large component of scats. The animals are apparently able to digest the organic material from bone, and in one winter the local population subsisted primarily on caribou remains that consisted only of bones and scraps of hide. "The wolverine's ability to survive the most severe time of the year on such a meager diet attests to its efficiency as a scavenger" (Magoun 1987).

2.4.2 Nutrition

Little is known about wolverine energetics, particularly in the field. As measured in the laboratory, wolverines appear to have a basal metabolic rate about 20% higher than would be predicted from body size (Iverson 1972a), and all accounts indicate that the young grow and develop very quickly (Davis 1967; Iverson 1972b; Shilo and Tamarovskaya 1981). Although the nickname "glutton" has commonly been applied to the species, suggesting an unusually voracious appetite, I found no clear evidence of gluttony as I understand it (i.e., over-eating) and Krott's (1960) opinion based on observations of several kept in captivity was that "...it shows no particular interest in new food opportunities after it has eaten..." The discrepancy in those views can likely be explained by the fact that human encounters with the species may most often be with very hungry individuals. Occasional and sometimes intense hunger is probably accessory to the scavenging lifestyle, particularly in winter, since each individual wolverine is largely reliant upon extrinsic forces (mostly climatic) and/or other carnivores (wolves, lynx, foxes) to provide the next meal. This point was emphasized by Banci (1987), who found that wolverine stomachs were often empty (about 23%, with no significant differences between animals that were "quick-killed" and those that

were restrained alive for a time in traps). Marked wolverines (old adults and young females) were known or suspected to have died of starvation in two of the four major North American field studies (Hornocker and Hash 1981; Banci 1987), and inadequate nutrition was believed to have resulted in widespread reproductive failure in a third (Magoun 1985). Further, hungry scavengers are believed particularly vulnerable to baited trap sets (Hornocker and Hash 1981).

On that point, it may be significant that Gardner (1985) had no luck capturing wolverines with livetraps in his southcentral Alaska study area, and had to resort to helicopter capture techniques to obtain his telemetry sample. Incidentally, his non-trapped males (all ages, but including many juveniles) had the highest average weight among the North American samples listed in Table 1. The most secure animals in good condition may be nearly untrappable in baited sets, and I believe that livetrapping studies therefore often involve study animals that are marginal representatives of the species.

Overall, as was the case for lynx, the actual values relating to food requirements, consumption, and metabolism are of only academic interest, but the level of nutrition may be of considerable management interest in its relationship to both the productivity and security of wolverine populations.

2.4.3 Activity

Haglund (1966) noted that the wolverine, with a daily activity pattern described as "irregular", was the most likely of the four large European predators to be seen during daylight hours. Folk *et al.* (1977) found little variation in daily activity patterns between seasons in a captive situation in arctic Alaska (despite great seasonal differences in day-length), and labelled the species "day-active" based on observations of increased activity in the morning with bouts of sleep at night. After much experience with free- ranging, partially domesticated animals, Krott (1960) concluded that the species is neither diurnal nor nocturnal, but rather tends to display alternating bouts of activity and rest (about 3-4 hours for each) in a more or less continuous pattern regardless of time of day. He noted that bad snow or rain storms tended to reduce or stop activity for up to several days, and that "certain favorable weather conditions" or extreme hunger might prolong it.

Daytime activity may be of benefit to wolverines in giving them access to cues such as raven activity to help locate carrion, and may reduce the chances for dangerous encounters with other large carnivores that may be more nocturnal in habits. From the standpoint of management, activity is probably of greatest interest in its relationship to trapping vulnerability.

2.4.4 Movements and Dispersal

Although the term "movements" includes dispersal in its generic meaning, it is used here primarily in reference to short-term activity within well-defined ranges, while dispersal includes the major, long distance and often longer term phenomena (e.g., emigration and immigration) that take individuals to new ranges.

Movements - Based on snow-tracking, wolverines have been characterized as extraordinarily active and nomadic. Haglund (1966) estimated 30 km as a "normal" daily movement, Pulliainen (1968) reported that females brought food to dens from up to 20 km away, and daily movements of 30-40 km from dens were known. On this continent, Scheffer (1938) noted that one observer followed fresh tracks for two days, from a location in Washington northward to the International Border (B.C.), without overtaking the animal. Movements of "...25 km...in several hours" and 25-30 km or more "...with no obvious signs of rests or pauses" were apparently documented in Mt. Assiniboine Prov. Park, B.C. (Cockerton and Herrero 1973, cited in Holbrow 1976). Judging from aerial observations of wolverine trails in several northern B.C. areas (Hatler, unpubl. obs.), such movements seem plausible, and based on calculated rates of travel for "unpursued" animals in Alaska (8.6 km/h for males and 4.6 km/h for females, Magoun 1985), they are certainly possible.

Telemetry results, expressed as straight-line distances between locations, tend to underestimate actual movements both because animal activity often follows meandering paths (actual movements averaged 33% more than calculated for monitored cases in arctic Alaska, Magoun 1985) and because a circuit out from and back to a particular location may be interpreted as only small or no movement. With those caveats, the maximum movements documented in Montana by Hornocker and Hash (1981) for a 3-day period were 64 km for males and 38 km for females. Average implied daily movements were considerably smaller, less than 2 km per day in all seasons, with males generally traveling farther than females, especially in spring and summer. In southcentral Alaska, the mean distance between locations (8-10 day intervals) for both summer and winter was about 13 km, again with males traveling about twice as far as females (Gardner 1985), while in northwestern Alaska the average daily distance between locations was 4.2 km for females and 12.3 for males, with maxima of 15.6 km and 35.6 km, respectively (Magoun 1985). For collared animals in the Yukon, daily movements averaged less than 1.5 km for most individuals, with the longest (17.3 km) by a male kit (Banci 1987).

While it is apparent that wolverines are capable of sustained activity that covers considerable ground over a relatively short period, the recent studies with known animals have demonstrated that such movements are not a regular daily feature of every individual's existence. Males generally travel farther than females, particularly in summer when each may be regularly monitoring several females for estrous condition (Magoun 1985). Mated pairs apparently travel very little during the 2-3 days they are together (Magoun and Valkenburg 1983). Movements and ranges of lactating females appear to be less extensive than those of other females (Hornocker and Hash 1981; Magoun 1985; Gardner 1985; Banci 1987), but the necessity for frequent return of mothers to natal dens or rendezvous sites may result in some of their movements being undetected.

Some animals have been documented to make long distance "excursions" away from established home ranges, returning some days or weeks later. In Montana, such movements were said to be "frequent" for individuals of both sexes (Hornocker and Hash 1981), while in the Yukon they involved all of three monitored females, and all in summer (Banci 1987). The purpose of those excursions is not known, but may relate to temporary reduced feeding opportunities in the home areas. The converse appears to be true--animals with adequate food supplies may be quite sedentary for a time. For example, a young male in southcentral Alaska was observed to remain

near a moose carcass for up to 27 days (Gardner 1985), and Banci (1987) believed that two males and one female on her Yukon study area also restricted their movements in response to the presence of ungulate kills.

That general pattern, an inverse relation between food availability and foraging effort (as reflected by extent of movements), is consistent with findings for lynx and with logical expectations. Clearly, movements are closely related to both activity and home range, and are of interest to managers for the same reasons. That is, animals that are nutritionally stressed or otherwise insecure will probably be more active, moving more and having larger ranges, and they are therefore more likely to encounter and fall victim to trap sets or come to conflict with man in settled areas.

Dispersal - All four of the North American telemetry studies documented apparent dispersal movements, mostly by young males. The longest involved an apparently transient 2-year old male that remained in the southcentral Alaska study area for at least 19 days after capture, then disappeared and was caught by a trapper 20 months later in Yukon Territory, 378 km to the east (Gardner 1985; Gardner *et al.* 1986). An ear-tagged female, believed to have been a yearling marked on Magoun's (1985) study area was trapped 300 km south less than 4 months later. Other recorded dispersals were shorter, involving animals that were trapped (possibly before completing dispersal movements) or those that stayed within the range of the telemetry searches and could therefore be relocated. Included in the former category was one juvenile male trapped 100 km south of his natal home range at the age of about 12 months (Magoun 1985), and another that dispersed in January (age 10-12 months) and was subsequently trapped 30 km northwest of his natal range (Gardner 1985). In addition, two young males (one juvenile and one subadult) were trapped after moving unspecified but apparently short distances north of the Yukon study area (Banci 1987), and trappers recovered apparently dispersing young (sexes not given) north, south, and west of the Montana study area (Hornocker and Hash 1981).

Although most of the cited studies indicated that juveniles began to show dispersal behavior, including occasional forays away from the natal range, in their first winter at about age one year, Magoun (1985) indicated that not all juveniles disperse at that time, if at all. In particular, females may often remain in or near the natal range for longer periods, and one was still present there at the age of 28 months. Local food shortage, agonistic interactions with the mother or other adults, and the effects of hormonal changes with the approaching breeding season have all been suggested as factors leading to dispersal movements, although both Gardner (1985) and Banci (1987) were inclined to rule out food shortage for the cases they observed. Dispersing juveniles that fail to find or establish permanent home ranges probably adopt a transient status, moving regularly in response to food availability and/or social pressures and showing the largest apparent home ranges and movements in the process. The longest dispersal described above is apparently illustrative of such cases, but it is likely that many of the extra-limital observations and pioneering appearances of "adult males" described under "distribution" (e.g., Scheffer 1941; Newby and Wright 1955; Newby and McDougal 1964; Patterson and Bowhay 1968; Yocom 1973; and others) were expressions of the same phenomenon.

As with lynx, the morphological uniformity of the wolverine across its continental range (Sections 2.2.1 and 2.2.2) is probably facilitated and maintained by widespread dispersal, which prevents the establishment of isolated gene pools. From a management point of view, dispersal can be thought of as a "natural transplant", and the existence of suitable refuges to disperse *from* is the mechanism most likely to prevent local extinctions and correct local declines.

2.4.5 Home Range

As an expression of activity and movements, home range has already been discussed at least in part in previous sections. The important thing to establish here is that the telemetry studies cited so often in these pages have confirmed that wolverines do exhibit fidelity to particular areas for months or even years. That conclusion may be contrary to the impression given by the movements of some individuals, which suggest a generally itinerant and nomadic existence. As was the case for lynx, data on home range sizes from radio-tracking vary considerably both between and within sex and age classes, locations, and seasons (Table 4). As discussed by Banci (1987), that variability is attributable partly to differences in presentation between studies, and partly to the different living circumstances of each contributing wolverine.

The general pattern depicted in Table 4, combining results for the four major North American study areas, is for males having larger ranges than females, and females without kits having larger ranges than those with. Most animals maintained different areas of activity in different seasons, and implied annual boundaries were not necessarily the same for each individual year after year. Banci (1987) has provided a detailed review and discussion of home range size, generally concluding that it tends to be inversely related to the availability of resources. Thus, as was the case for lynx, home range size is probably of interest to managers only indirectly, in the degree to which it may reflect environmental conditions and/or the relative stability and density of local populations. Large ranges may indicate relative sparsity of resources, usually food, and/or may reflect a relative absence of social interactions because of low density. The data in Table 4 serve primarily as an order-of-magnitude preview of values and variations that can be expected.

2.4.6 Health

The parasitological literature was searched by title and not by index, therefore some broad surveys that included wolverine only as one of several species examined or as one of several hosts of a particular parasite may have been missed. Table 5 lists parasites recovered and identified in the few analyses I am aware of. There have apparently been only two studies involving collections of several fresh specimens. One or more gastro-intestinal helminths were found in 38 of 39 wolverines (97%) from the Northwest Territories (Addison and Boles 1978), and in 69 of 80 (86%) specimens from Alaska (Rausch 1959). The observed infection rate for *Trichinella* in muscle tissue varied considerably between the two studies--0 of 38 for the NWT sample as opposed to 19 of 39 (49%) in Alaska. A single specimen from Iowa was also found to harbour trichina larvae.

Table 4. Home range sizes of adult wolverines in North America, as determined by radio telemetry studies

Location	Season[1]	Sample[2] N	T	DTA	Home Range Sizes (km2) Male	Female	Both	Range	Lit.[6]
Montana	T	1	D	U		963		-	1
	A	11	V	402		388		-963	1
	S	2	U	U		100[3]		-	1
	A	9	V	174	422			-	1
NW Alaska	S	11	V	404		94		38-318	2
	S	3	V	U		70[3]		55- 99	2
	S	5	V	U		97[4]		68-178	2
	A	10	V	549		104		53-232	2
	S	4	V	114	626			488-898	2
	A	4	V	137	666			488-917	2
	S	3	V	74	49[5]			41- 55	2
	A	3	V	107	53[5]			46- 58	2
Southcentral Alaska	A	1	D	40	637			-	3
	W	1	U	U	515			-	3
	S	1	U	U	451			-	3
	W	5	V	52	353			69-515	3
	W	4	V	78	385			92-451	3
	S	1	B	18		92[3]		-	3
	T	4	V	U	535			-	4
	T	3	V	U		105[3]		-	4
Yukon	A	2	V	63		273[4]		202-343	5
	A	1	C	39		139[3]		-	5
	A	2	C	50	382			238-526	5

[1] Seasons: W=winter (about November through March); S=summer (about April through October); A=annual (year round); T=Total (whole sample period, potentially results for several seasons and more than one annual cycle).

[2] Sample Characteristics - N=Number of animals; T=tracking period (A=1-30 days, B=31-180 days, C=181-365 days, D=366+ days, U=unspecified, V=variable); DTA=Data Points (number of locations or U=unspecified);

[3] Females with young. [4] Females without young. [5] Juveniles.

[6] Literature Sources: 1) Hornocker and Hash (1981), 2) Magoun (1985), 3) Gardner (1985), 4) Whitman *et al.* (1986), 5) Banci (1987).

Table 5. Some parasites of wolverine in North America, as recorded in the literature

Parasites[1]	Incidence of Parasites[2]						
	Alaska		NWT	B.C.	Other		
	A	B	C	D	E[3]	F[4]	G
NEMATODA							
Trichinella sp.	M-4-3		M-4-0		M-1-5		
Physaloptera sp.			G-4-1		M-1-5		
Physaloptera torquata	G-5-2						
Baylisascaris devosi	G-5-2		G-4-4				
Skrjabingylus nasicola						S-3-0	
Molineus patens	G-5-1						
Soboliphyme baturini							G-U-U[5]
CESTODA							
Taenia twitchelli	G-5-4	G-1-5	G-4-3				G-1-5[6]
Taenia martis			G-4-2				
Diphyllobothrium sp.			G-4-2				
Mesocestoides kirbyi	G-5-1						
TREMATODA							
Alaria sp.			G-4-1				
SIPHONAPTERA							
Chaetopsylla setosa				E-U-U			
Thrassis spenceri				E-1-5			
Oropsylla sp.		E-1-5					

1 Parasite names as presented by the authors indicated.

2 Incidence of parasites - 3 letter/number codes, as follows:
First - Organ infected (G=gastro-intestinal tract, L=lungs, H=heart, M=muscle, S=skull, E=external, U=unspecified). Second - Number of wolverine specimens (1=1, 2=2-10, 3=11-25, 4=26-50, 5=51+, U=unspecified). Third - Infection rates (frequency) - 1=<5%, 2=5-25%, 3=26-50%, 4=51-75%, 5=76-100%, U=unspecified).
Literature Sources: A) Rausch (1959), B) Philip (1938), C) Addison and Boles (1978), D) Holland (1941, 1949), E) Haugen (1961), F) Swales (1938), G) see footnotes 5 and 6, below.

3 Iowa

4 "Canada" (sample of museum specimens, the negative information is listed here because the parasite is common in mustelids and has been reported from wolverines elsewhere (Hansson 1970, in 1 of 102 specimens).

5 Personal communication reports of incidences in Montana and "Canada" to Rausch (1959).

6 Personal communication report from Jasper National Park area, Alberta, to Rausch (1959).

The most frequent and widespread of the helminths identified is a cestode, *Taenia twitchelli*, whose life cycle is believed to include wolverine as the primary host and the porcupine as the "essential intermediate host" (Rausch 1959), thereby suggesting a regular predator-prey relationship between those two species. The "true host" of one of the fleas identified on a wolverine specimen (*Thrassis*) is another wolverine prey species, the hoary marmot (Holland 1949). The nematode *Skrjabingylus nasicola* commonly infects the sinuses of mustelids, at rates and with sufficient skull damage so that population effects are possible. It therefore may be significant that only 1 of 102 European wolverine skulls (Hansson 1970) and none of 19 Canadian skulls (Swales 1938) showed evidence of sinus worm damage. Ritcey and Edwards (1958) listed the wolverine as a "suspected host" of the hydatid tapeworm *Echinococcus granulosus* in the Wells Gray Park area, British Columbia, but there are no documented cases. In summary, I found no published records of any chronic diseases or parasite disorders that might have implications for wolverine populations.

There is evidence, as was the case for lynx, that the factor most often contributing to declining physical condition of individual wolverines is nutrition. The species' ecological position as a "...seasonal scavenger on the fringe of the main links of the food web" (Van Zyll de Jong 1975) can be a precarious one, with individuals relying on winter foraging opportunities that are unpredictable at best (see discussions in Banci 1987 and Magoun 1985). Deaths by starvation were reported in both the Montana (Hornocker and Hash 1981) and Yukon (Banci 1981) studies, and reproductive failure among all collared females was documented following a particularly difficult winter for wolverines in northwestern Alaska (Magoun 1985). An old adult female that died during the Yukon study was diagnosed as having "...protozoal cysts in diaphragmatic and skeletal muscle, parasitic pneumonia and focal interstitial nephritis." That animal's poor condition was also believed to have had a nutritional basis, relating to the demands of caring for her young (Banci 1987). Based on that observation and on the apparent starvation losses of two female kits, Banci (1987) speculated that "inexperienced and old wolverine may not be efficient at securing food even if availability is high."

Patterns of change in physical condition are of potential management interest as indicators of differential trapping vulnerabilities between sex and age classes and/or in different time periods. Based on a kidney fat index (KFI), Rausch and Pearson (1972) found that Yukon wolverines (N=61) appeared to be in the best physiological condition in spring (March-April) and poorest in summer (May-September). They speculated that spring is generally the period of highest food availability, particularly in the form of ungulate carrion, and that the reproductive cycle is timed accordingly. In their comparisons, the sexes did not differ significantly in KFI, and data were not categorized by age or by time periods within the trapping season. In a subsequent and considerably larger sample of winter-trapped Yukon specimens (N=459, Banci 1987), the KFI was ruled out as a useful indicator of condition. Although the results were not shown, they were described as very variable by parametric comparisons, with no apparent patterns attributable to sex, age, year, or month. Visual estimates of total body fat (low, medium, high) showed more females (21%) than males (10%) in the low category, but most animals (69%) were rated medium, and there were no apparent differences among age classes, months, or years.

As for lynx, it is likely that some animals are held alive in traps longer than others, with probable varying effects on their apparent condition after death, and that comparisons of condition indices for trapped samples should therefore be interpreted conservatively. Also as for lynx, it seems reasonable to expect that older, more experienced and secure animals would maintain better condition than newly independent young and most transients, that males would generally do better than females that produce and feed young, and that all classes would do more poorly with the advance of at least some winters and/or with decreasing food availability. Failure to demonstrate those patterns for wolverines to date may be because a) they do not apply to that species, b) the samples are biased (e.g., most animals in poor condition die before they are trapped and/or those in good condition are rarely trapped), or c) a suitable technique for quantifying condition is yet to be developed.

2.4.7 Pelage

The pelage of the wolverine has received some attention because of its durability and apparent frost-shedding characteristics (Hardy 1948; Quick 1952), but there appear to be no publications relating specifically to the biological aspects of fur growth, e.g., the annual moult cycle. Davis (1967) noted that two young born in captivity were "pure white" at birth, but were in pelage resembling that of the adults by the time they were 3 months old (mid- May). Based on extensive literature review and interviews with fur graders, Stains (1979) concluded that the average period of pelt primeness for the species is from about early December through February, but with maximum primeness in December and January. He acknowledges that there may be some variations in that pattern due to factors such as nutrition, weather conditions, and differences in life cycle schedules by latitude. As with lynx, it is likely that there are also differences in primeness patterns by sex and age, but they have not yet been described.

2.4.8 Denning

There is little information on the daily bed-sites of wolverines, but like lynx they apparently most often use suitable locations along the daily travel route rather than repeatedly returning to any particular site. Two beds located by Pulliainen and Ovaskainen (1975) included one on snow "between a birch and a stone" at the bottom of a ravine, and one "...near a tree in a small spruce stand between two fells." During snow-tracking studies in Montana, Hornocker and Hash (1981) found beds "...in snow, on open outcrops...all in timber types which afforded cover." Wolverines also construct and use snow caves and tunnels, especially near ungulate kills and other large supplies of carrion (Haglund 1966).

Descriptions of natal dens used by wolverine are more common than was the case for lynx, no doubt because the young are born in late winter when the dens can be located by snow-tracking. Following are summaries for several areas within the Holarctic range of the species:

- Finland: As generalized by Krott (1959b), "...in mountain areas...often a cave or cleft in the rock, but in the forest may be a hollow in a snowdrift under a fallen tree or under thick blowdown."

- Finnish Lapland: Of 31 natal dens located by bounty hunters, 25 (81%) were in generally rocky (fell) habitats and the other 6 were in spruce or pine peat bogs; those in rocky terrain included 10 (32% of the total) in deep ravines, 8 (26%) on gentle slopes near timberline, and 7 (23%) in subalpine or alpine habitats; all but one were under deep snow, in tunnels up to 30 m long, and most were snow chambers at ground level; where present, fallen trees often formed the ceiling of the nest chamber; 17 of the dens were found in northern Lapland, where there were apparently no trees, while 8 of 14 found in the taiga of northeastern Lapland used tree structures in some way (Pulliainen 1968).

- Sweden: Dens were most commonly snow caves amid rock formations in the mountains, but occasionally below timberline in rocky slide areas (Haglund 1966).

- Alaska: Two of three dens observed were above timberline in snow- filled ravines, and one was in an abandoned beaver house. Moose carrion was available near both ravine sites (Rausch and Pearson 1972).

- Northwestern Alaska: All natal dens examined in this tundra habitat were in tunnels and caves dug 1-2.5 m below the surface of the snow; associated terrain features, if any, were not described (Magoun 1985).

- Montana: "Natal dens...are most commonly associated with snow- covered tree roots, logjams, or rocks and boulders" (Hash 1987).

In general, the common feature of most of the sites described above is snow cover, and that is not likely to be limiting in the appropriate season in most areas of British Columbia. Although trees are often incorporated in the structure of dens, it is clear that they are not essential. Thus, there does not appear to be any specific "critical habitat" that can be identified for protection of denning opportunities.

2.4.9 Behavior

The primary management-oriented interest under this heading relates to the species' social organization, and the degree to which territorial behavior may limit population size. As described in a previous section (2.4.5), individual wolverines may establish and maintain distinct areas of use (home ranges), and the important question here is whether those areas tend to be mutually exclusive. The primary evidence on the subject is mostly indirect, based on the nature and extent of range overlap observed among marked animals. Applicable findings from each of the four intensive North American studies are as follows:

- Montana: considerable range overlap both between and within sexes, and no evidence of strict territorial defense by agonistic behavior (Hornocker and Hash 1981, Hornocker *et al.* (1983).

- Northwestern Alaska: little overlap between females except in the case of mother/daughter situations, complete overlap of males and females, and too little data to ascertain whether male ranges were exclusive (Magoun 1985).

- Southcentral Alaska: too little data to ascertain spatial relationships between females, but there was generally little overlap between males (Gardner 1985).

- Yukon Territory: overlap between sexes, but insufficient data to ascertain patterns within sexes (Banci 1987).

Difficulties in determining the residency status of some individuals and lack of knowledge about the familial relationship of adjacent individuals have both been cited as impediments to interpreting territorial relationships strictly from observations of range overlap (Hornocker and Hash 1981; Gardner 1985; Magoun 1985). The evidence to date, however, suggests that the general spacing pattern for the wolverine, as for several other mustelids, is of the "intrasexual" type, with considerable home range overlap between and little within the sexes (Powell 1979). Male ranges are generally larger, especially in summer when breeding occurs, and may contain the ranges of several females, e.g. an estimated 4-6 in northwestern Alaska (Magoun 1985). It is speculated that female spatial organization is determined primarily by the distribution of food, but that of males is determined primarily by the distribution of females (MacDonald 1983; Magoun 1985).

Although the contrary results in Montana (overlap within as well as between sexes) may have been due to the sample bias/interpretation problems mentioned above, it has also been suggested that the study population was subject to such rapid turn-over that local individuals did not have time to develop a "full territorial system" (Hornocker and Hash 1981). Further, the above authors, Hornocker *et al.* (1983), and Banci (1987) have all called attention to some practical difficulties and logical inconsistencies of a strict territorial system for this species. In particular, it is noted that for the large ranges required by the scavenging lifestyle, territorial maintenance would be very difficult and, given the unpredictability of food availability in some seasons, possibly unrewarding. Hornocker *et al.* (1983) concluded that the wolverine has a "flexible" behavioral system that "...may be regarded as a positive adaptation to different and changing environments and is of value to the species survival." In any case, it is apparent that the situation is similar to that described for lynx in the sense that an individual's need for food may supersede boundary considerations. For example, although adult females were shown to be the class with the most exclusive ranges in Magoun's (1985) study, one of those made frequent excursions into the ranges of other females in one winter, apparently because of "impending starvation".

Topics relating to territoriality and spacing strategies (above) were indexed under the term "socbehav" in the bibliography (Part 3). Many of the papers under the broader heading of "behavior" were simple narrative accounts of interactions between humans and wolverines, mostly referring to loss or damage of property. Other aspects of behavior that may have management implications are discussed briefly in following paragraphs:

Scent marking - Wolverines produce and distribute a variety of odorous substances that are believed to be important in communication. The secretion from the prominent anal glands appears to be used primarily in fear/defense situations, while urine and musk from the ventral abdominal gland are the substances most-used in ritualized scent marking behavior (Long 1987). Scratching the ground and biting tree limbs or roots are sometimes also associated with scent deposition (Koehler *et al.* 1980). In addition, Buskirk *et al.* (1986) have described structures on the hind feet (plantar glands) which they believe may be used in "passive chemical communication", broadcasting the animal's presence whenever the hind feet contact some object in the environment. Observations during snow-tracking (Pulliainen and Ovaskainen 1975, Koehler *et al.* 1980, Magoun 1985) confirm that scent-marking is a frequent, conspicuous, energy-demanding activity among free-ranging wolverines, although there is some indication that transients may mark less than residents (Banci 1987) and possibly females less than males (true in Koehler *et al.* 1980, but not in Magoun 1985). Scent marking is generally regarded as relating to social organization and spacing behavior, although it seems clear that chemical signals cannot and do not prevent trespass. Koehler *et al.* (1980) speculated that its primary function is to maintain time rather than area spacing, by indicating that an area is occupied and thereby facilitating avoidance by others.

Foraging Behavior - Biologists engaged in wolverine studies by snow-tracking have noted that the impression given by a foraging animal is that it is simply "looking for something to eat" rather than "hunting" in the usual sense (Haglund 1966; Hornocker and Hash 1981). As indicated by many of the anecdotes involving wolverine depredations on traplines (e.g., see MacIver 1952), and documented more officially by snow-tracking and direct observations (Krott 1960; Haglund 1966; Magoun 1985), food storing (caching) behavior by burying food remains in snow or soil is common. Much of the winter foraging in some areas may consist primarily of animals locating and digging up caches made by themselves, other wolverines, or other carnivores such as red foxes (see Magoun 1985). Evidence from tracking indicates that wolverines commonly follow the tracks of lynx, foxes, and wolves (Haglund 1966; Makridin 1964; Pulliainen and Ovaskainen 1975; Magoun 1985; Gardner 1985), presumably in hopes of finding remains cached or left by those species. Depredations on traplines and human supply caches is probably a manifestation of that natural foraging behavior. Further, and of particular relevance to management, that behavior is believed to make wolverines particularly vulnerable to baited trap sets (Hash 1987).

Behavioral Flexibility - Based on many years observation of semi-captive animals, Krott (1960) developed considerable respect for the wolverine's "intelligence". He described the species as very cautious and suspicious by nature, with the ability to learn and change behavior as required, and considered its "...extraordinary ability to evade dangers...(to be)...far superior to any other northern mammal, including the wolf". Anecdotes and legends relating to the behavior of "trap shy" individuals (see Holbrow 1976) lend some popular support to that suggestion.

2.5 POPULATION DYNAMICS

2.5.1 Cycles

A major feature of lynx biology is the 10-year population cycle, following that of its primary prey, the snowshoe hare. In a mathematical analysis of historic and recent fur returns, Bulmer (1974, 1975) concluded that the wolverine was subject to the same cycle, also in response to hare abundance, but with peaks and troughs following those of lynx by 3-4 years. He postulated that the "phase lag" was due to characteristics of wolverine reproduction, particularly delayed implantation. However, he also acknowledged that the apparent relationship to the lynx/hare cycle might be an artefact of sampling, with the wolverines becoming easier to trap when hares were scarce. No other students of historic fur sales and furbearer cycles have featured wolverines in their discussions. Indeed, an analysis of 19th century fur returns from British Columbia years earlier (Cowan 1938) had resulted in the conclusion that "...no relation can be traced between fluctuations in (wolverine) numbers and the rabbit cycle." Holbrow (1976) cited both fur production data (western Canada) and results of numerous trapper interviews as evidence against population cycling in the species. It is evident that population fluctuations occur, but apparently not in any regular, predictable pattern.

2.5.2 Natality

A major feature of wolverine reproduction, delayed implantation, was first confirmed for the species from a small sample of Alaska specimens (Wright and Rausch 1955). That and subsequent studies and observations at several locations in the North American range have indicated that mating occurs in summer, at least late May through early August but perhaps mostly in June, and that the young are born in winter, apparently mostly in February and March (Rausch and Pearson 1972; Liskop *et al.* 1981; Magoun and Valkenburg 1983; Magoun 1985; Krott and Gardner 1985; Banci 1987). The extended mating season is probably necessary to ensure that estrous females are located by the more widely dispersed males, and ovulation may be of the induced type (Magoun 1985). Pregnancy after implantation is believed to last 30-40 days (Rausch and Pearson 1972), but the total gestation period may be variable--two cases observed in captivity were calculated at 215 and 272 days (Mehrer 1976).

There are two important points relative to the winter parturition: 1) It is believed to be keyed to the time when ungulate carrion is likely to be most available (Rausch and Pearson 1972; Banci 1987), thereby suggesting the importance of local ungulate populations in wolverine population dynamics and, 2) most of the later stages of pregnancy, including birth in at least some cases, occur during the trapping season.

Table 6 summarizes some aspects of wolverine reproductive performance throughout the Holarctic range, as determined from post-mortem examination of female specimens and observations of live litters. Results of ovarian analyses (mainly counts of corpora lutea) are generally ignored here, since they suffice only to confirm the obvious--that some early *in utero* losses occur during the species' long pregnancy. As is generally the case for the larger mustelids (Erlinge 1986), the

potential of the species is rather low, with delayed maturity and small litter size. The earliest breeding among females occurs in their second summer, when they about 1.5 years old (subadults), and the first young may be produced on about their second birthday. However, as was also the case for lynx, the pregnancy rate in the first breeders class is apparently quite variable, ranging from as low as 7% in a sample from the Yukon (Banci 1987) to as high as 85% in a smaller sample from British Columbia (Liskop *et al.* 1981). Incidence of pregnancy is also somewhat variable among adult females (at least 2 years old at breeding), with about one/fourth of those from the Yukon and British Columbia failing to show reproductive activity during the years they were trapped (Table 6). Considering the presence of non-pregnant adults, the fact that breeding occurs in summer when females are still accompanied by young and presumably still lactating, and the general lifestyle, it had been suspected that individual female wolverines might not breed every year (Makridin 1964; Ewer 1973). However, observations in arctic Alaska showed that consecutive year breeding may occur whether or not kits were produced in the previous year (Magoun and Valkenburg 1983; Magoun 1985).

Based on embryo and fetus counts, litter sizes as high as six are possible, but I found no reference to live litters larger than four and the average in all areas has been less than three. The most detailed observations relating to reproductive output of live animals are from the extreme arctic environment of northwestern Alaska (Magoun 1985). Based on records for six radio-collared adult females monitored over a 5-year period, the "reproductive rate" (kits produced) was 0.69/female/year. Adding the results for two subadults, neither of which produced kits, that figure is 0.60/female/year. Differences between females were evident, with one averaging 1.25 kits/year over a 4-year period (3 years with kits), while another produced no kits in three years. There were also differences between years, with one or more of one to four monitored adults producing young in 4 of 5 years, but none of five successfully doing so in the other. In the only other study that tabulated results by year (Rausch and Pearson 1972), fetus counts ranged from 2.6 in 1962 (N=5) to 5.2 in 1966 (N=5).

The two factors that seem most likely to influence productivity of individual females, the availability of males and aspects of nutrition, are discussed separately below:

Effect of Males - Given that males are believed more vulnerable to trapping than females (Section 2.6.2), it is conceivable that removal of resident males could result in failure to breed among females within those males' former territories. However, the 5-6 months period between the end of trapping season and the end of the breeding season provides good opportunity for recolonization by the widely ranging transient males. Histological studies indicate that, as with females, males may become sexually mature as subadults (Rausch and Pearson 1972; Banci 1987), thus at least some transients would be capable as replacements for resident adults. Lack of males would be expressed in reproductive performance by reduced incidence of pregnancy. As listed in Table 6, 10-25% of female reproductive tracts were inactive, but none of the available pregnancy data were tabulated in such a way (e.g., by location or year) to indicate patterns that might relate to male abundance. The failure of some females to produce kits in Magoun's (1985) study was suspected to have been due to unsuccessful pregnancies and/or early losses of kits (rather than failure to breed). In general, the role of male availability in wolverine productivity is unclear.

Table 6. Aspects of reproductive performance in the wolverine, as recorded in the literature

LOCATION			Litter Sizes						
	PP/PG[2]		*In Utero*			In Den or Later			
Age Class[1]	%	(N)	Mean	Range	(N)	Mean	Range	(N)	LIT[4]
FINLAND									
N/S	-	-	3.0	1-5	(2)	2.4	1-4	(73)	1
EURASIA[3]									
N/S	-	-	-	-	-	2.5	1-4	(161)	1
ALASKA									
Mature	-	-	3.5	3-4	(2)	-	-	-	2
Kits	0	109	-	-	-	-	-	-	3
Subadults	50	40	-	-	-	-	-	-	3
Adults	92	98	-	-	-	-	-	-	3
Mature	-	-	3.5	1-6	(54)	-	-	-	3
Mature	-	-	-	-	-	1.8	1-2	(5)	4
YUKON									
Kits	0	82	-	-	-	-	-	-	5
Subadults	7	27	-	-	-	-	-	-	5
Adults	73	79	-	-	-	-	-	-	5
Mature	-	-	3.2	2-4	(23)	-	-	-	5
B.C.									
Kits	0	16	-	-	-	-	-	-	6
Subadults	85	13	-	-	-	-	-	-	6
Adults	77	13	-	-	-	-	-	-	6
Mature	-	-	2.6	-	(5)	-	-	-	6
Montana									
Mature	-	-	2.2	-	(6)	-	-	-	7

[1] Age classes (Age in most recent breeding season): Kits = less than 1 year; subadults = between 1 and 2 years; adults = at least 2 years; N/S = not specified; mature = at least 1 year (subadults and adults combined).

[2] PP/PG - Females either post-partum or pregnant.

[3] Based on 116 litters from Finland, 38 from Sweden, and 7 from the U.S.S.R.

[4] Literature Sources: 1) Pulliainen (1968), 2) Wright and Rausch (1955), 3) Rausch and Pearson (1972), 4) Magoun (1985), 5) Banci (1987), 6) Liskop *et al.* (1981), 7) Hornocker and Hash (1981).

Effect of Nutrition - The failure of all collared arctic wolverines to produce kits in 1980 was believed due to the scant winter food opportunities in that year (Magoun 1985, 1987). In addition, Banci (1987) emphasized the unpredictability of winter food supplies and suggested that "...adequate food during pregnancy was the most critical factor governing reproductive success." In particular, she speculated that the energetic demands of raising young may "...reduce the probability that a female...will successfully reproduce the next year", and that "...females may not implant unless they are in sufficiently good condition to maintain pregnancy." Again, other than the suggestive between-year variability in fetus counts documented by Rausch and Pearson (1972), there is little relevant information.

The hypothesized relationship between nutrition and productivity is strongly reminiscent of the situation that has been described for lynx. Based on the previously described rigors of wolverine existence, it seems likely that for any given female wolverine in any particular year the local nutritional regime might approximate that of a hare low to a lynx. Occasionally, such as in the year of reproductive failure described by Magoun (1985), many or all local animals might be faced with existence at that marginal subsistence level. Banci (1987) had difficulty measuring and demonstrating differences in condition among her large sample of specimens, and although females were assigned low condition indices more often than males, there were apparently no differences in apparent condition between reproductive and non-reproductive females.

From the only data available for British Columbia (Table 6), Liskop *et al.* (1981) concluded that "...the reproductive rate appears to be lower" than in other areas of North America. However, that conclusion appears to be based only on somewhat smaller corpora lutea and *in utero* litter counts in a small sample of animals, and does not take into consideration that the frequency of pregnancy in subadults was apparently far higher than recorded in other areas. Those data suggest that, as for lynx, the class of first breeders may be more successful in some years and/or areas than others, possibly again related to patterns of food availability. In addition, there is some evidence that productivity (as measured by corpora lutea counts) increases with age up to at least age 5 (Banci 1987), thus a young sample might be expected to show a lower reproductive rate.

A final point in consideration of the available data on wolverine reproduction is that if, as seems likely, the animals with the least secure food supplies are the most vulnerable to trapping, and if reduced food supply is also reflected in reduced reproductive output, then results from analysis of trapped specimens may be somewhat pessimistic.

2.5.3 Mortality

Table 7 summarizes aspects of mortality documented for radio-collared wolverines in North America. Trapping and hunting accounted for most of the observed losses, and mostly involved transient and/or dispersing young males. The incidence of documented harvest loss for all telemetry studies combined was 14% (10 of 73), considerably less than the 85% documented for lynx. Characteristics of the wolverine harvest by humans is described and discussed in more detail in Section 2.6.2. There is little direct information on the extent or causes of natural mortality in the wolverine. The most frequent single cause among the collared animals was starvation, and three of the four losses known or suspected due to that cause were juvenile females--the smallest class in the sample. Young-of-year females show less tendency than young males to disperse, usually

remaining in or near their mother's home ranges (Magoun 1985). Such behavior is believed to have socio-biological implications and advantages, but it may result in a local competitive and food-finding disadvantage in some cases. It appears that the proximate cause of death for the old adult female that died in captivity in the Yukon (Banci 1987) also was, or would have been, starvation, and an adult female in northwestern Alaska was believed to have been "...on the verge of starvation" in late winter of the poor food year (Magoun 1985).

Table 7. Fates of radio-collared wolverines and incidental observations of natural mortality in unmarked wolverines in North America. The figures in the body of the table refer to the number, age, and sex of documented mortalities (AM and AF=adult males and adult females, including subadults; JM and JF=young-of-year males and females; U=sex and age unknown or not specified

OBSERVATIONS	Sample (N) ADULT		JUV		Incidence and Causes of Mortality					
Location	M	F	M	F	Harvest	Starve	Wolf	Other	Unknown	Lit[10]
RADIO-COLLARED ANIMALS										
Montana	9	8	2	5	5U	1AM,1JF	-	1AF1	-	1
NW Alaska	8	4	8	4[2]	2AM,1JM	-	-	-	-	2
SC Alaska	5	2	3[3]	-	1AM,1JM 2U[4]	-	-	-	1AM[5]	3
Yukon Terr.	4	3	1	2	2AM	2JF[6]	1JM	1AF[7]	-	4
INCIDENTAL										
Alaska							1F[8]			5
Yukon Terr.							1AM			4
NWT							1AM,1AF[9]			6
NWT							1U			7

[1] An "old-appearing female, diagnosed as dying from "suppurative metritis"; "the uterus was badly infected and contained decomposed tissue, possibly a retained fetus".

[2] Female sample also included 2 for which age was not determined.

[3] Male sample also included 3 with age unknown.

[4] Both males, and one possibly a juvenile.

[5] Cause of death not known, but the animal had been partly eaten and cached by another wolverine.

[6] One known and one suspected dead by starvation.

[7] This old adult female first sustained an injury, apparently a bite by a wolf, and although the wound healed, declined in condition and eventually died in captivity. It was diagnosed as having "parasitic pneumonia" and a kidney disease, but the author believed that the energetic demand of caring for young was a major contributing factor in its death.

[8] The animal was reportedly small, possibly a juvenile.

[9] The female was young (age 2) and was killed while restrained in a trap.

[10] Literature Sources: 1) Hornocker and Hash (1981), 2) Magoun (1985), 3) Gardner (1985), 4) Banci (1987), 5) Burkholder (1962), 6) Boles (1977), 7) Gill (1978).

Six wolverines, including one of the collared animals in the Yukon study area, have been documented as killed by wolves (Table 7), and one other in Banci's (1985) study was believed to have been injured by a wolf. At least three of the mortalities were at or near wolf-killed ungulates that were being scavenged, thus such encounters appear to constitute another wolverine foraging hazard. About half of the wolf-killed wolverine found by Gill (1978) had been eaten, but very little of the others reported above were consumed. It appears likely that they were killed primarily in defense of food sources, although possibly they were killed as prey and then found unpalatable. Following an observation of a wolverine being treed by dogs, Grinnell (1920) suggested that the use of trees as refuge from wolves might be a regular part of the wolverine's behavioral repertoire. In support of that hypothesis, the Alaskan naturalist Adolph Murie is cited as observing three instances of wolverines being pursued by wolves, with the wolverines escaping in each case by climbing trees (Boles 1978), and in the incident reported by Burkholder (1962) the wolverine attempted, unsuccessfully, to climb some small poplars in the area. Krott (1957, 1960) believed that the wolverine's association with the boreal forest and its natural wariness are evolutionary dictates of wolf presence. Although wolves occurred in Magoun's (1985) study area north of the treeline, they were not present in winter when the wolverines were scavenging and no mortalities or injuries were documented in that area.

Wolves were not present in the Montana study area, but one wolverine there was believed to have been injured twice in encounters with cougars. There is too little information to speculate on the population implications of wolverine interactions with larger carnivores, but it appears that a dynamic tension exists, with the wolverines both dependent upon them for food and in danger from them as predators and competitors.

2.5.4 Population Abundance and Composition

As noted by Gardner (1985), inventory of wolverine populations over large areas such as management units would be difficult, and is probably impractical. Most of the papers documented under "poptrend" in the bibliography provide only general statements of abundance, with the terms "rare" and "scarce" appearing commonly, and probably applicable more to the species natural (ecological) occurrence than to population trend. It is generally believed that wolverine populations in eastern North America declined in historic times and have not recovered (Dagg and Campbell 1974b; Van Zyll de Jong 1975). However, there is evidence for increases and range expansions in the mountains of the west over the last few decades, particularly in Montana (Newby and Wright 1955; Newby and McDougal 1964) and in Washington and Oregon (Johnson 1977; Yocom 1973, 1974). In the context of this report, dispersal from viable populations in British Columbia appears to have contributed to those northwestern U.S. increases.

The first numerical estimate for population density in North America appears to be that of Quick (1953b). Based on a combination of catch data and track counts along a sample of trapline trails, he calculated a pre-trapping population of about 250 animals for his 51 200 km² study area in northern British Columbia (1 wolverine/207 km²). However, the more intensive studies conducted in the past decade have generally found higher densities, as follows:

Hornocker and Hash (1981) used recapture data, telemetry, and snow- tracking to identify a minimum of 20 wolverines on their 1300 km² Montana study area (1 wolverine/65 km²).

Magoun (1985) used average summer home range size, extent of range overlap, and reproductive performance observed among collared resident animals to derive fall population estimates of 1 wolverine/48 km² in the foothills region of GMU 26A in northwestern Alaska, and 1 wolverine/139 km² if the adjacent coastal plain region were included. Those estimates were considered conservative in that they did not account for transient animals over 1 year old.

In the 1590 km² Yukon study area monitored by Banci (1987), a minimum density of 1 resident wolverine/177 km² (3 adult males and 6 adult females) was calculated. She also used harvest data to calculate "productivity indices" by ecoregion, and from those statistics estimated a total Yukon wolverine population of about 4380 animals.

The above accounts confirm that wolverines occur at relatively low densities, but that there may be considerable variation between locations and probably between years. In terms of management, the general difficulty in accounting for transients in population estimates is significant, since that class may be particularly important both in the harvest and in population maintenance (Hornocker and Hash 1981; Magoun 1985).

There is little direct information on the sex and age composition of wolverine populations. As indicated in the reproduction section (2.5.2), young-of-the-year were not a conspicuous component of any of the telemetry study populations, but samples were small. Based on capture data, Hornocker and Hash (1981) concluded that the sex ratio of their study population was about 1:1. Adult females exceeded males by 2:1 in the Yukon study (Banci 1987) and an estimated 4-6:1 in northwestern Alaska (Magoun 1985). The latter author noted that since male home ranges are so much larger than those of females, there are fewer male ranges and males therefore remain in transient status more commonly and for longer periods.

2.5.5 Population Regulation

The role of social behavior in limiting population size is unclear, but the Montana studies seem to indicate that territoriality may function primarily in facilitating avoidance between animals (Koehler *et al.* 1980), and that strict maintenance of territories would be impractical both because of the large home range sizes involved and because of the uncertainty of food supplies associated with the scavenging lifestyle (Hornocker *et al.* 1983). The timing of parturition relative to ungulate vulnerability patterns (Rausch and Pearson 1972; Banci 1987) and the apparent relationship of productivity to scavenging opportunity (Magoun 1985) tend to confirm Kelsall's (1981) conclusion that the primary limiting factor for the wolverine is food availability, particularly in the form of large, viable populations of local ungulates.

2.6 POPULATION MANAGEMENT

2.6.1 Economic Considerations

In British Columbia, as in most jurisdictions supporting viable populations, the wolverine is managed primarily for commercial use as a furbearer (Munro and Jackson 1979). Table 8 outlines the pattern of economic returns from wolverine trapping in the province since 1950. For perspective, it should be noted that British Columbia has consistently been the Number 1 wolverine producer in Canada over at least the past decade (Table 9), during which time the average price for pelts has remained fairly steadily at its highest ever level (about $200). For most of that period, the proportion of total provincial fur sales attributable to wolverine was less than 2%, while the highest (4.0-4.5%) was in the years 1974-77. That period directly followed the 1970's harvest peak for lynx, and the higher wolverine harvests at that time may reflect increased incidental catches in trap sets intended for the higher valued and more easily handled lynx. In addition, the increased proportional value of the mid-1970's wolverine harvest is at least partly related to the diminishing contribution of lynx at that time.

Some of the papers indexed under economics in the bibliography (Section 3) are negative in that context, referring to depredations by the animal. Wolverines have been observed to kill caribou and reindeer (Burkholder 1962; Haglund 1966; Filinov 1980; Magoun 1985), moose (Grinnell 1920; Haglund 1974; Filinov 1980), elk (Grinnell 1926), and Dall's sheep (Gill 1978), and one was observed in an unsuccessful attack on a mountain goat in British Columbia (Guiguet 1951). However, it is generally believed that most actual predation by wolverines involves severely incapacitated ungulates, and that such predation is insignificant in ungulate population dynamics. Gill (1978) held a contrary view, observing that a wolverine that killed a young sheep in the Northwest Territories had used an attack strategy that suggested "learned predatory behaviour", and that the dead sheep was apparently the last (or only) one of that age class in the local herd. He therefore surmised that late winter wolverine predation on sheep might be more important, at least in that area, than has commonly been thought.

Depredations by wolverines on human property and traplines in wilderness areas are a well-established part of the species' mythology and lore, but there is little documentation of the extent of such damage that can be expected over any given time period. Based on reports from trappers in the Fort Nelson area of northern British Columbia, Quick (1953b) concluded that wolverines caused less damage and loss of furs than wolves during his study years, and that "...in some years shrews cause more damage than either wolves or wolverines." Holbrow (1976) has conducted the most thorough research on the subject, compiling questionnaire results from 394 trappers throughout western Canada. Damage estimates amounted to an average of about $250 per year, with only a portion of that due to wolverines. Only 128 of 394 trappers (32%) had ever experienced damage by wolverines (63 of 178 = 35% in B.C.), and only 31 of 153 (20%) felt that wolverines were a negative factor in the local fur industry (13 of 54 = 24% in B.C.). Nevertheless, many trap sets for wolverine may be motivated as much by the risk of depredations as by the value of the fur.

Table 8. Value of wolverine (Wv) pelts and harvests in British Columbia, 1950-1987[1]

Trapping Season	No. Wv Sold	Average Value ($)	Wv Total Sales ($)	Total Fur Sales ($) (All Species)	Wv Proportion (%)[2]
1949-50	96	8.95	859	949,975	0.1
1950-51	329	25.90	8,521	1,589,223	0.5
1951-52	203	15.26	3,098	812,466	0.4
1952-53	163	13.51	2,202	708,688	0.3
1953-54	145	10.66	1,546	567,785	0.3
1954-55	172	16.38	2,817	774,570	0.4
1955-56	136	15.70	2,135	572,595	0.4
1956-57	147	18.00	2,646	399,117	0.7
1957-58	140	8.75	1,225	393,345	0.3
1958-59	134	15.36	2,058	421,694	0.5
1959-60	180	15.00	2,700	812,080	0.3
1960-61	143	15.00	2,145	646,538	0.3
1961-62	149	15.00	2,235	629,558	0.4
1962-63	40	18.53	741	922,357	0.1
1963-64	214	14.24	3,047	763,562	0.4
1964-65	241	19.32	4,656	778,339	0.6
1965-66	195	28.00	5,460	776,542	0.7
1966-67	257	28.65	7,363	671,061	1.1
1967-68	314	32.56	10,224	805,551	1.3
1968-69	274	47.97	13,144	649,969	2.0
1969-70	356	31.57	11,239	647,561	1.7
1970-71	411	64.91	26,678	682,035	3.9
1971-72	306	81.50	24,939	742,430	3.4
1972-73	505	94.41	47,677	1,741,680	2.7
1973-74	634	82.98	52,609	1,883,893	2.8
1974-75	508	118.73	60,315	1,349,773	4.5
1975-76	455	177.75	80,876	1,832,071	4.4
1976-77	424	199.82	84,724	2,095,691	4.0
1977-78	383	180.11	68,982	2,109,335	3.3
1978-79	275	200.06	55,017	3,627,909	1.5
1979-80	283	166.33	47,071	4,035,574	1.2
1980-81	225	202.78	45,626	3,633,304	1.3
1981-82	214	186.10	39,825	3,382,737	1.2
1982-83	265	182.12	48,262	3,827,978	1.3
1983-84	265	226.70	60,076	3,584,709	1.7
1984-85	260	215.67	56,074	4,890,771	1.2
1985-86	210	235.38	49,430	3,172,599	1.6
1986-87	246	183.58	45,161	5,798,571	0.8
1987-88	221	182.84	40,408	-	-

[1] Data for 1949-50 through 1985-86 from Statistics Canada Records (Fur Production of Canada Series), and 1986-87 from files of B.C. Ministry of Environment, Wildlife Branch, Victoria).

[2] Percentage of total B.C. fur sales due to wolverine.

Table 9. Geographical distribution of the wolverine harvest in Canada, 1976-1985

	Number of Wolverines Reported, By Year[1]									
	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
Alberta	52	96	80	85	74	99	80	103	49	89
British Columbia	455	424	383	275	283	225	214	265	265	260
Manitoba	31	36	45	74	103	94	128	141	67	92
New Brunswick	-	-	-	-	-	-	-	-	-	-
Newfoundland	-	-	-	-	-	-	-	-	-	-
Northwest Terr.	86	68	86	78	110	60	88	137	107	129
Nova Scotia	-	-	-	-	-	-	-	-	-	-
Ontario	-	6	11	18	9	9	22	26	11	9
Prince Edward I.	-	-	-	-	-	-	-	-	-	-
Quebec	3	6	3	6	1	-	-	-	-	-
Saskatchewan	8	21	36	28	32	29	33	22	25	23
Yukon Terr.	236	268	182	210	165	93	110	336	205	229
Totals:	871	925	826	774	777	609	675	1030	729	831
	Proportion of Year's Harvest/Rank[2]									
Alberta	6/4	10/3	10/3	11/3	10/5	16/2	12/5	10/5	7/5	11/4
British Columbia	52/1	46/1	46/1	36/1	36/1	37/1	32/1	26/2	36/1	31/1
Manitoba	4/5	4/5	5/5	10/4	13/4	15/3	19/2	14/3	9/4	11/4
New Brunswick	-	-	-	-	-	-	-	-	-	-
Newfoundland	-	-	-	-	-	-	-	-	-	-
Northwest Terr.	10/3	7/4	10/3	10/4	14/3	10/5	13/4	13/4	15/3	16/3
Nova Scotia	-	-	-	-	-	-	-	-	-	-
Ontario	-	1/7	1/7	2/7	1/7	1/7	3/7	3/6	2/7	1/7
Prince Edward I.	-	-	-	-	-	-	-	-	-	-
Quebec	-	1/7	-	1/8	-	-	-	-	-	-
Saskatchewan	1/6	2/6	4/6	4/6	4/6	5/6	5/6	2/7	3/6	3/6
Yukon Terr.	27/2	29/2	22/2	27/2	21/2	15/3	16/3	33/1	28/2	28/2

[1] Data from Statistics Canada Records (Fur Production of Canada Series), Ottawa.

[2] The number to the left of the diagonal is the percentage of total harvest for the year indicated, while the number to the right is the rank, from 1-x, where 1 is the highest wolverine producer.

By all accounts, the economic value of the wolverine is not high. Thus, as noted by Hash (1987), wolverine populations "...seldom warrant high priority on the agenda of wildlife agencies charged with managing many species." The low overall economic value is due primarily to the animal's low density occurrence, and therefore its inability to supply large numbers. That is true for the individual trapper as well as for large administrative areas. As stated by one trapper interviewed by Holbrow (1976), "If a guy had to depend for a living on all the wolverine he caught, he'd be one hungry S.O.B."

2.6.2 Harvest Characteristics

Numbers - Figure 1 depicts the pattern of reported wolverine harvests in British Columbia since 1920. Clarke (1944) noted that many of the wolverine skins obtained by natives in the northern Northwest Territories were imported from British Columbia, and based on information obtained in the Fort Nelson area, Quick (1953b) stated that "...wolverine pelts are often kept by the trapper and/or sold privately at other than normal outlets." It is unclear whether, how much, or how long such practices may have affected historic wolverine harvest reporting, thus little can be said about the reliability of the early data (i.e., through at least the 1950's and possibly longer). Figure 2, which shows average pelt prices and harvests since 1950, shows a roughly parallel relationship between those two parameters through the mid-1970's, but with price following rather than leading harvest trend. The 1970's peak corresponds to generally increased prices for all furs, generating renewed interest in trapping and probably increasing both direct and incidental pressure on wolverines as a result.

British Columbia had generally been categorized as one of few jurisdictions that had not experienced significant changes in wolverine distribution and/or production in this century (Dagg and Campbell 1974b; Van Zyll de Jong 1975; Holbrow 1976). However, following three consecutive seasons of wolverine yields exceeding 500 animals (1973-75), there was a steady decline to an average of 238 (range 210-265) for 1980-87, despite a relatively high average pelt price throughout that period. One interpretation of that pattern might be that the peak harvests in the mid-1970's were excessive, resulting in population decline. In the absence of comparative information on the distribution and composition of harvests, trapper effort, and aspects of natality and food availability, confirmation or refutation of that interpretation is difficult. The peak reported harvest of 634 animals for the 1973-74 season would be 8-13% of the grossly estimated provincial population (5000-8000, Munro and Jackson 1979), and most other harvests are 10% or less of the estimated lower limit. In the most recent assessment of wolverine harvests in British Columbia, Liskop *et al.* (1981) expressed no concern over the increase in the mid-1970's, commenting only that they believed it was due to "increased accessibility".

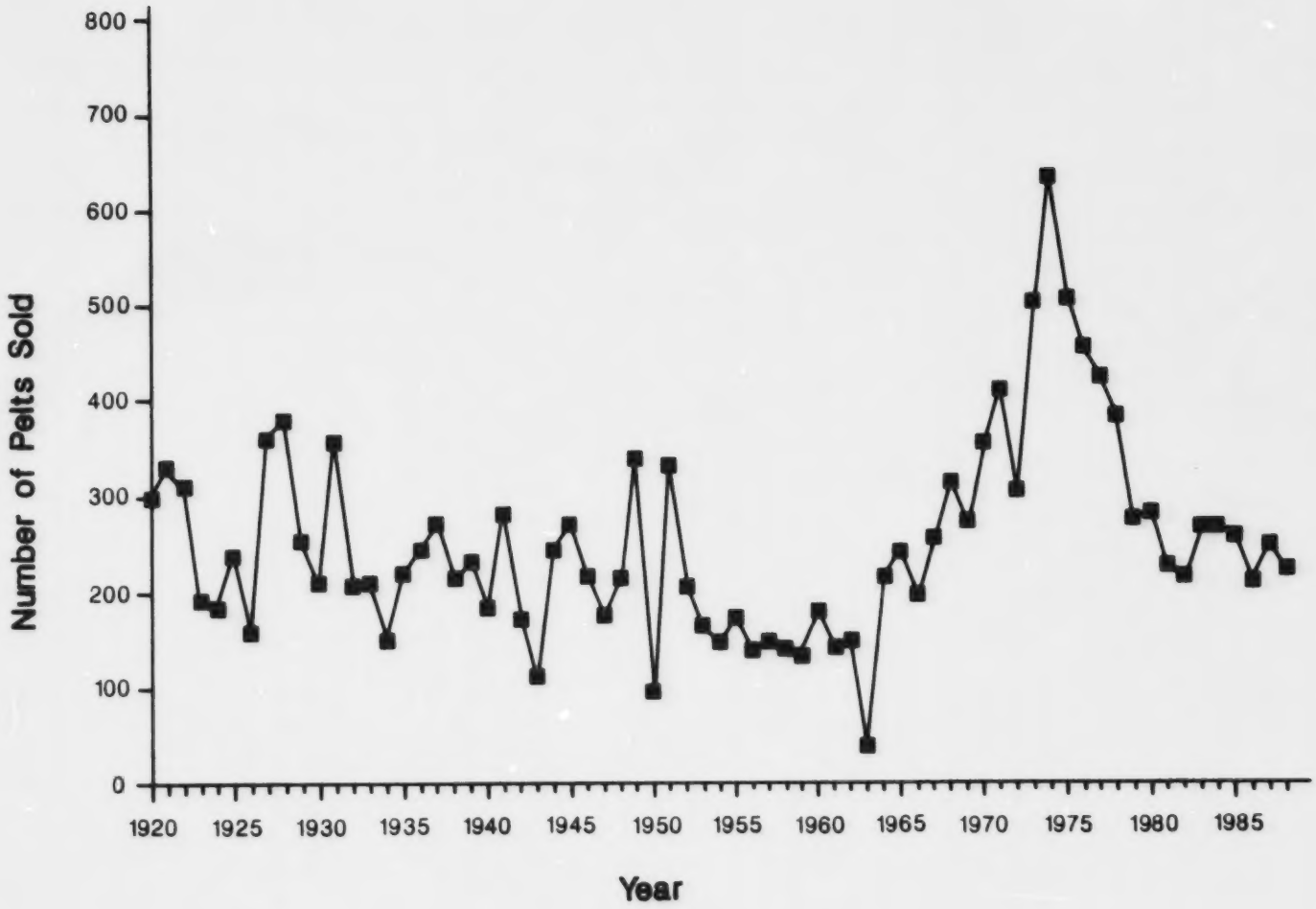

Figure 1. Reported harvest of wolverines in British Columbia, 1920-1987.

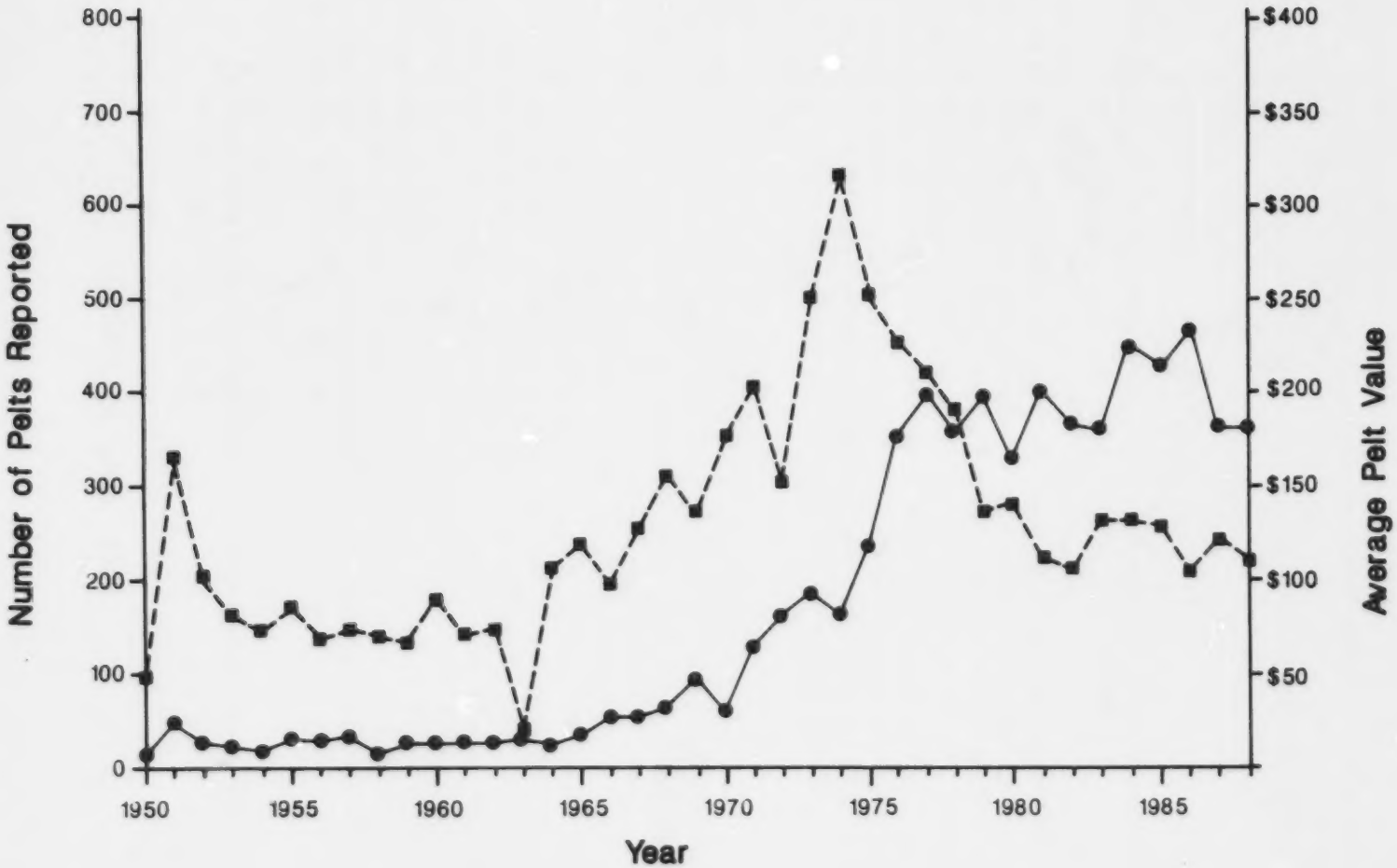

Figure 2. Wolverine harvests in relation to average pelt value in British Columbia, 1950-1988.

Harvest Distribution and Dispersion - Wolverine harvest data for British Columbia have been compiled by location only over the past three years. As shown in Figure 3, the bulk of the reported harvest has come from the Omineca- Peace and Skeena Regions, which collectively constitute the northern half of the province, while the third highest production has consistently come from the Kootenay Region, in the southeast. Tables 10-12 provide additional perspective on the distribution and dispersion of recent harvests. During the three sample years, slightly more than half of the 218 management units (M.U.'s) in the province produced one or more wolverines (Table 10). No wolverines were reported for the two southwestern regions (Vancouver Island and Lower Mainland), and they will not be discussed further here. Within regions, the frequency of successful (wolverine-producing) M.U.'s ranged from 30% in the Thompson-Nicola to 86% in the Omineca-Peace, although not all such M.U.'s supported wolverine harvests every year. In more than a third of them, province-wide, wolverines were taken in only one of the three years, with the highest frequencies in that category generally in the southern regions. The Skeena Region ranked highest in consistency of production, with 50% of its successful M.U.'s providing yields in all three years.

Annual local harvests were generally low, with nearly half of all M.U.s producing just 1 wolverine and only about 20% of them producing more than 3 (Table 11). The 11 M.U.'s producing a total of 10 or more wolverines over the 3-year period were well dispersed, occurring in 7 of the province's "ecoregions" (Table 12). There appeared to be little variation between years at the provincial level, with the reported yield per successful M.U. over the three sample years calculated at 2.21, 2.46, and 2.51 pelts, respectively (mean = 2.39). The time available for this project did not allow consideration of trapper numbers and activity, or differences in M.U. and trapline sizes. All of those factors would probably influence mean local harvests, thus the results presented above should be considered as preliminary only.

As the M.U. results would suggest, the annual catch by individual trappers was also generally small, with almost 70% consisting of a single wolverine and only 12% exceeding 2 animals (Table 13). Banci (1987) reported that over 85% of the registered traplines in the Yukon Territory reported nil wolverine harvests, thus it is likely that the average catch for all active trappers in B.C. is much smaller than the 1.5 per successful trapper indicated in Table 13.

The number of wolverines taken by hunters (as opposed to trappers) is also apparently small. Compulsory inspection records indicate that for the calendar years 1986 and 1987, the total non-trapping kill was two (in two different M.U.'s of Omineca-Peace) and three (one each in Thompson-Nicola, Kootenay, and Skeena), respectively (Data secured by D. Steventon, B.C. Wildlife Branch, Smithers).

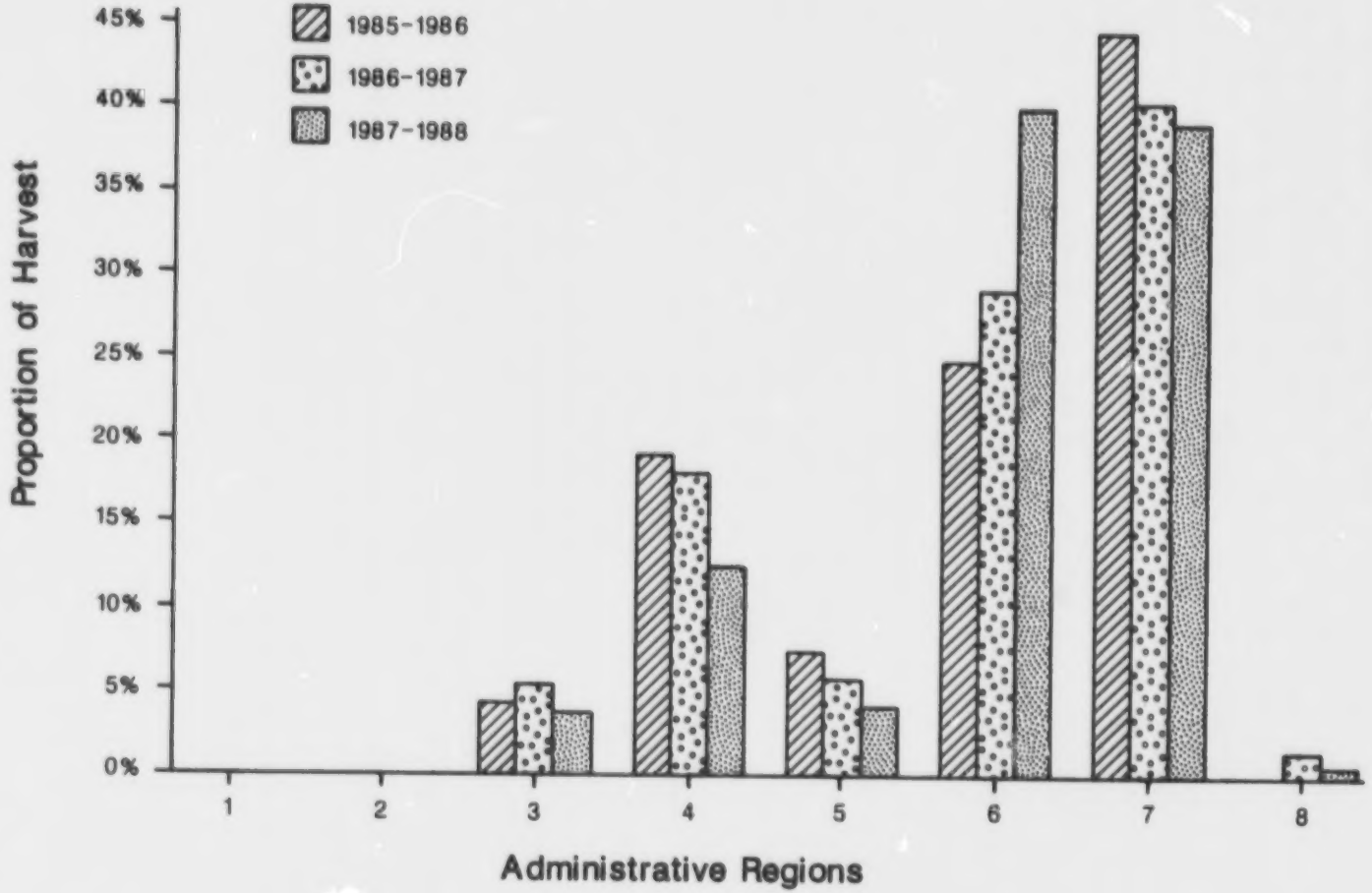

Figure 3. Regional distribution of the wolverine harvest in British Columbia, 1985-86 through 1987-88. Regions and subregions: 1 = Vancouver Island; 2 = Lower Mainland; 3 = Thompson-Nicola; 4 = Kootenay; 5 = Cariboo; 6 = Skeena; 7 = Omineca-Peace; 8 = Okanagan.

Table 10. Distribution of the reported wolverine harvest in British Columbia, 1985-86 through 1987-88

Admin. Region	Number M.U.'s	Wolverine Producers[1]		M.U. Harvest Frequencies[2]					
				1 Year Only		2 of 3 Years		All of 3 Years	
		No.	%	No.	%	No.	%	No.	%
Vancouver Island	15	0	0	-	-	-	-	-	-
Lower Mainland	15	0	0	-	-	-	-	-	-
Thompson-Nicola	30	9	30	5	56	4	44	0	0
Kootenay	36	25	69	11	44	6	24	8	32
Cariboo	15	8	53	3	38	2	25	3	38
Skeena	30	24	80	7	29	5	21	12	50
Omineca-Peace	56	48	86	15	31	19	40	14	29
Okanagan	21	3	14	2	67	1	33	0	0
ALL	218	117	54	43	37	37	32	37	32

[1] Management units (M.U.'s) producing at least one wolverine during the three-year period.

[2] Management units producing 1 or more wolverines in one, two, or all of the three years indicated.

Table 11. Reported harvest frequencies for wolverines by management unit in British Columbia, 1985-86 through 1987-88

Admin. Region	N[1]	Freq. (%) for Number of Wolverines/M.U./Year									
		1	2	3	4	5	6	7	8	9	10+
Thompson-Nicola	13	62	15	8	15	0	0	0	0	0	0
Kootenay	47	62	11	12	11	2	0	2	0	0	0
Cariboo	16	50	19	19	6	6	0	0	0	0	0
Skeena	53	31	25	15	5	5	8	2	2	5	2
Omineca-Peace	95	46	23	8	8	6	5	0	0	1	1
Okanagan	4	100	0	0	0	0	0	0	0	0	0
ALL	228	48	20	11	8	5	4	1	<1	2	1

[1] Number of M.U.'s producing one or more wolverines per year over the three year period (some M.U.'s represented more than once).

Table 12. Distribution, yearly production, and broad ecological affinities of British Columbia Management Units (M.U.'s) producing 10 or more wolverines over the 3-year period, 1985-86 through 1987-88

M.U.	No. of Wolverines Reported				Ecoregion[1]
	1986	1987	1988	Total	
7-03	13	6	6	25	Southern Rocky Mountains
6-04	8	5	9	22	Fraser Plateau
6-25	1	9	11	21	Northern Mountains and Plateaus
6-09	4	3	9	16	Fraser Plateau
7-38	-	5	9	14	Skeena and Omineca Mountains
6-20	1	6	6	13	Northern Mountains and Plateaus
6-26	1	6	5	12	Northern Mountains and Plateaus
4-26	5	4	2	11	Columbia Mountains and Highlands
5-04	3	4	4	11	Chilcotin Ranges
4-34	2	7	1	10	Columbia Mountains and Highlands
7-51	1	5	4	10	Northern Rocky Mountains

[1] from Demarchi, D.A. 1988. A regional wildlife ecosystem classification for British Columbia. Pages 11-19 *in* H.A. Stelfox and G.R. Ironside (eds). Land/Wildlife Integration No. 3, Ecol. Land Classification Ser. No. 22, Land Conserv. Branch, Can. Wildl. Serv., Ottawa.

Table 13. Annual harvests of wolverines by individual trappers in British Columbia, 1985-86 through 1987-88

Admin. Region	N[1]	Freq. (%) for Number of Wolverines/Trapper/Year					Total Wolverines	Wolverines Per Trapper[2]
		1	2	3	4	5+		
Thompson-Nicola	15	66	20	2	2	0	23	1.53
Kootenay	71	76	20	4	0	0	91	1.28
Cariboo	23	70	26	0	4	0	32	1.39
Skeena	98	63	18	8	4	6	172	1.76
Omineca-Peace	147	69	19	7	3	2	226	1.54
Okanagan	4	100	0	0	0	0	4	1.00
ALL	358	69	19	6	3	3	548	1.53

[1] Number of trappers producing one or more wolverines per year over the three year period (trappers with catches in more than one year are represented more than once).

[2] Mean number per successful trapper per year, i.e., not including results for trappers who reported catching no wolverines.

Harvest Composition - In a sample (recalculated) of 576 carcasses taken over a 7-8 year period in Alaska, Rausch and Pearson (1972) found sex ratios varying between age classes, with males constituting 56%, 67%, 82%, and 64% in age classes 0 (kits) through 3, respectively, but with approximately equal ratios for older classes (ages 5-12 combined). They speculated that the nearly even sex ratio among kits was due to their not having established territories and therefore being equally trappable at that age, the prevalence of young males (ages 1-3) resulted from their larger ranges and movements, and the equal ratio among older animals may have reflected "...a reduction of males through exploitation." Magoun (1985) also found a predominance of males in the northwestern Alaska harvest, particularly among animals taken late in the season by shooting after tracking from aircraft or snowmobiles. She noted that females with young were less vulnerable at that time than other classes because of their more restricted activity around den sites, but thought that they would remain at least equally vulnerable to trap sets within their areas of activity. She also suggested that male ranges are in shorter supply than female ranges because they are so much larger, therefore males are likely to remain transients (with greater vulnerability) longer than females.

In southcentral Alaska, the recorded harvest over three seasons also included more males (58%), although a small sample (N=51) for which ages were determined showed a seasonal pattern by sex and age, as follows:

November	-	mostly female kits.
December	-	male kits and subadults predominating.
January	-	sexes equal, mostly kits and subadults.
February	-	mostly young males, but adult female component increasing.
March	-	sexes equal, all age classes but mostly kits and subadults.

A large collection (N=462) of trapped Yukon wolverines was biased to males in all of three years, but differed significantly from 1:1 only in one of those years (69% males) and in the combined sample (58%). The seasonal pattern in that sample is difficult to interpret because the statistical comparisons involve "expected" values that are not adequately explained, some plotting errors apparently occurred, and trends are shown only within rather than between sex and age classes. The author's interpretation (Banci 1987) was that male kits showed the clearest seasonal trend, with their highest harvest in the first half of the season (peaking in January). Subadult males and females peaked in February, the latter ostensibly becoming more vulnerable at that time because of increased nutritional demands for raising young. There were no clear peaks for the other classes, although the graphs show slight trends to predominance in the early part of the season for female kits and subadults, and a general increase throughout the season for adult males.

Kits (young-of-the-year) and subadults (yearlings) together have predominated in trapped samples in all of the studies in which ages have been determined, as follows:

Location	Sample Size	Proportion of Harvest (%) Kits	Subadults	Adults	Source
Alaska	576	42.0	19.8	38.2	Rausch and Pearson (1972)
B.C.	86	34.9	27.9	37.2	Liskop *et al.* (1981)
Alaska	51	43.1	29.4	27.5	Gardner (1985)
Yukon	413	33.4	18.2	48.4	Banci (1987)

The adult component in the above studies includes large numbers of 2-year olds, especially males, which the telemetry studies indicate are often in the "transient" category (Section 2.4.4), and would also include "old" animals in poor condition such as those described in Section 2.5.3. Thus, the actual proportion of the "secure" residents harvested would appear to be less, possibly considerably less, than the figures in the adults column might suggest.

Hash (1987) reported that wild wolverines harvested in Montana rarely exceeded 8 years of age, and the average was 4-6 years, but Magoun (1985) reported cementum ages of 9 years for one male and two females and up to 11 years for one female in northwestern Alaska. Tabular listings in Banci (1987) also indicate at least one female aged 11+ in the Yukon sample, while in southcentral Alaska only 2 of 35 males (both age 7) and 4 of 25 females (6,6,7,9) exceeded 5 years of age. The largest age samples are from the study of Rausch and Pearson (1972) where, among 576 animals from Alaska (mostly trapped) and 142 from the Yukon Territory (mostly taken at predator control bait stations), 95% were 7 years old or younger, and only 1% were 9 or older (to a maximum of 13).

It seems generally agreed that the sex and age data from harvest samples usually cannot be relied upon to directly reflect the composition of the population. Rather, they tend to indicate differential vulnerabilities of the various sex and age classes under the environmental and harvesting conditions pertaining (Magoun 1985; Banci 1987). Previous sections have emphasized the role of nutrition in wolverine biology, with the animals' activity, movements, condition, and productivity all showing relationships to food availability. As with lynx, and probably most other carnivore furbearers, the least secure animals nutritionally will likely be the most vulnerable to trapping at any given time, and that will usually be juveniles and/or transients before adults and/or residents. Information presently available suggests that the vulnerability of adults is most likely to increase with advanced age and with the progressing winter (more in some years than others, and particularly for pregnant or lactating females). The primary management implications of within-season harvest composition changes are that a) managers may be able to select and/or protect certain classes by altering season dates, and b) harvest comparisons between areas and between years may not be valid if different trapping seasons are involved.

2.6.3 Harvest Management

British Columbia furbearers are classified into three management categories in relation to individual home range sizes and perceived differential vulnerability to harvesting (R. Archibald, personal communication):

Class 1 - Those furbearers present on Registered Traplines (RTL's) in manageable numbers (i.e., those for which harvest regimes can effectively be established by the trapper).

Class 2 - Those furbearers not present on (most) RTL's in manageable numbers, and which are vulnerable to overharvest.

Class 3 - Those furbearers not present on RTL's in manageable numbers, but not subject to overharvest (wolves and coyotes only).

Wolverines are Class 2 species, and the stated management strategy is to apply harvest regulations (e.g., restrictive seasons and/or quotas) at the management unit or regional level.

For the 1987-88 year, the open season for wolverine trapping was 3 months long (15 November - 15 February) in most southern administrative regions, but was 2 weeks longer (opening 1 November) in Thompson-Nicola, and was 4 months long (1 November - 28 February) in all of Omineca-Peace and all of Skeena except for three coastal M.U.'s. No bag limits or quotas were in effect, except that the season for the Vancouver Island Region applied only to its two mainland units, i.e., there was no open season on Vancouver Island proper. An open wolverine season for hunters, under a "small game" designation, ran concurrently with the above trapping seasons in Thompson- Nicola and Kootenay, but was open for only 1 month in Skeena (15 October - 15 November), and two seasons applied in Omineca-Peace (15 October - 15 January, = 4 months in three southeastern, six central, and nine northern M.U.'s, and 1 November - 15 February, = 3.5 months in all remaining M.U.'s). A bag limit of one and compulsory inspection requirement applied to those hunting seasons.

There has been no monitoring of British Columbia wolverine populations, either by field indices or by questionnaire. The main harvest monitoring in the past was at the pelt sales level, mostly involving only a province-wide tabulation of numbers. In recent years, trappers have been required to identify fur shipments and sales with assigned "Trapper Numbers", to enable compilation of harvest data by geographical units within the province. As yet, there has been no attempt to compile kill information by sex or age except for the small, well-dispersed sample of Liskop *et al.* (1981).

From the review information presented in preceding sections, the following are considerations that appear most relevant to the topic of a wolverine management strategy for British Columbia. In that context, the major positive life history and population dynamics features for wolverines are probably that they often occupy rugged, remote uplands that are difficult of access and rarely subject to competing human land uses, they do not appear to suffer high natural mortality, their mobility and dispersal tendencies reduce the likelihood of local extirpations, and they are nowhere

abundant enough or valuable enough to be intensively sought by trappers. The major negative feature also relates to the general rarity of the species, which makes it difficult to monitor population status and trend. Intuitively, the relatively low reproductive rate and the occurrence of parturition during the trapping season seem negative for management, but there is no evidence that either is a factor at the level and dispersion of current harvests in British Columbia.

Although more data on the subject are required, there is evidence that vulnerability to trapping varies relatively predictably among sex and age classes, and that physical condition related to nutrition might be a common underlying vulnerability factor within classes. Thus it appears that there is a level of trapping that tends to select for the least secure (and probably least productive) individuals. Since some of those individuals have been known to starve (Section 5.3.3), such trapping mortality is at least partly compensatory.

Following are some specific management options and activities that may be applicable for particular areas of British Columbia:

1) Manipulation of Season Length - Given evidence that trapping pressure might be too heavy, the most promising management response would appear to be shortening the season *at the end*, thereby providing protection for resident males and productive females before they reach their maximum seasonal vulnerability. Closure after January, as recommended by Hash (1987), would probably be the most protective regulation for females with kits.

2) Bag Limits and Quotas - Since few trappers catch more than 1 or 2 wolverines in a season, bag limits or quotas higher than zero seem of little potential value for significantly reducing harvests of this species in most areas of the province. Zero quotas (closed seasons) are potentially applicable for enhancing recovery of greatly depressed populations in areas with low immigration potential. Note that where trappers are actively seeking other species, incidental catch of wolverines may occur.

3) Methods and Means - Hornocker and Hash (1981) and Hash (1987) suggested the curtailment of baited trap sets for all species in areas where expansion of wolverine populations is desired. Such a regulation would be impractical for the trapper and would be difficult to enforce over most of British Columbia. Further, if there is indeed a difference in response to baits between animals of different sex and age classes and/or residential status, bait sets are the most likely to produce compensatory harvests.

   There is an interesting irony in regard to present regulations requiring the use of killer type traps (e.g., the 330 conibear) for use on the species. The ability of wolverines to escape from leghold traps is legendary. For example, Quick (1953b) reported that of 44 wolverines known to have been held in such traps in his study area, only 27 (61%) were killed, the remainder escaping. As reported in Holbrow (1976), some trappers indicated a belief that most "trap-shy" wolverines were such escapees. Specifying use of humane traps therefore appears to preclude providing for an "educated" and therefore more secure segment of a local population.

4) Hunting Closures - The harvest by non-trappers under B.C. "small game" regulations does not appear significant at current levels, but most probably occurs incidentally around the remains of hunter-killed ungulates in the fall and may not be selective for any particular class of animal, i.e., may be largely additive mortality. Thus, for areas where a reduction in trapping pressure is deemed desirable, adjustment of local hunting regulations is probably also warranted.

5) Refuges - The recovery and maintenance of wolverine populations south of the Canadian border are thought to have been made possible largely by dispersal from refuges, in the form both of areas protected by law (e.g., national parks), and those protected in fact by their remoteness and relative inaccessibility (Section 2.2.3). It is likely that maintenance of British Columbia's premier position for wolverine production in Canada has been enhanced by the refuge effect provided by large areas of inaccessible and rugged mountain wilderness. In that context, increased access for resource development will tend to reduce wolverine population security. The best option for management, given the fact of such access, will be for trappers to resist exploiting all areas that become accessible, essentially establishing refuge areas within their traplines. In particular, areas of apparent intensive local use in late winter may signal occurrence of a natal den, which would be best protected.

6) Transplants - Although not likely required or applicable to any area of British Columbia in the near future, reintroduction of the species to formerly occupied areas is a potential remedial measure. A release ratio of 2-4 females per male is recommended (Hash 1987).

2.6.4 Harvest and Population Monitoring

More intensive wolverine management in British Columbia will require more intensive monitoring. Although harvest information is limited in the degree to which it can document population status and trend, it is nevertheless needed to better describe the extent and distribution of trapper demand and the biological characteristics of the supply. To enhance comparability, local (trapline) or regional harvest objectives and production would be better expressed on some area-based system such as "harvest density", rather than in absolute terms for the various, different-sized administrative units (see previously cited lynx report for details).

A complete review of specimen analysis procedures cannot be provided here, but there are some important generalities. Young wolverines grow and mature quickly, and older animals may differ in condition and productivity, such that age cannot reliably be determined for winter-caught specimens by gross features such as body size, external examination of reproductive organs, or tooth wear. Annuli in dental cementum are apparently less distinct and more difficult to interpret for wolverines than for many other species (Banci 1987), but that technique is generally accepted as the most accurate means for determining year class at this time (Magoun 1985; Gardner 1985; Hash 1987). Sex can accurately be determined by skull measurements (see Magoun 1985).

Study of female reproductive tracts also appears to be less straight- forward and rewarding than for other species, particularly in the case of ovarian analyses (Rausch and Pearson 1972; Banci 1987). Fetus and placental scar counts give a measure of reproductive potential, but it seems to be generally agreed that prenatal and early juvenile mortality may occasionally be high in this species (Magoun 1985; Banci 1987; Hash 1987), thus the study of uteri may not provide a reliable indication of actual recruitment. Based on a relatively small sample of reproductive tracts, Liskop *et al.* (1981) suggested that British Columbia wolverines may have a lower reproductive rate than those elsewhere. Thus, there is some basis for additional research on the subject in this province, but reproductive analysis does not appear promising as an ongoing population monitoring technique for management.

Condition indices, which are important as they relate to recruitment and aspects of vulnerability to trapping, have been assessed by subjective evaluations or measurement of various fat deposits (Rausch and Pearson 1972; Banci 1987). The latter author was pessimistic about the usefulness of the kidney fat index or subjective assessments of total body fat (see Section 2.4.6), and no alternative methods for evaluating condition have been developed.

The collection of harvest data has improved greatly in British Columbia in recent years, providing more accurate information on numbers taken and, for the first time, enabling compilation by location. However, such information can provide no clear understanding of population status and therefore no indication of management needs. The available information reviewed above suggests that the best relative measure of recruitment is likely to be the proportion of young animals in the harvest, while a preponderance of adult females (either generally or in some particular time period) may suggest a need for management attention. Due to the pressure of prioritizing, management agencies tend not to collect data on a particular species until there is some cause, such as suspicion of declines. For wolverines in particular, there is a need to establish some long-term "baseline information" on sex, age, and temporal patterns in the harvest, as related to patterns of numbers and environmental parameters (e.g., climate). Without such information, data collected later, in response to alarm, will be difficult to interpret.

As recommended by Magoun (1985), collection of skulls appears to offer the best potential for gathering the required information, accurately and efficiently providing data on both sex and age but without burdening trappers to the extent that carcass collections do. It should be noted that date of kill, an important datum for wolverines in relation to their winter parturition schedule, is not presently collected.

Given the natural sparseness of wolverine populations, their widespread distribution in the province, their relatively low economic value, and the lack of any "alarming" data relative to population trend, field surveys to determine numbers or indices of relative abundance (e.g., by winter track counts) are not practical, even if possible. Official knowledge about the wolverine remains low in British Columbia, and I believe that the most promising source of information for the immediate future is the collective experience of trappers, who are at least as widely distributed as the wolverines. Both questionnaires and interviews will be required.

2.7 HABITAT MANAGEMENT

In general, too little is known about the wolverine's specific habitat predilections, either generally or seasonally, to ascertain whether protection or enhancement of any particular types or components are required. The animals are often associated with conifers, particularly at high elevation (Section 2.3), but the general impression is that physiography and vegetation are less important, *per se*, than the quantity and availability of local food resources. It has been suggested that maintenance of large, viable ungulate populations (winter food) and large areas of wilderness (refuge) are the primary requisites for maintaining wolverine populations (Van Zyll de Jong 1975; Kelsall 1981; Magoun 1985). However, it is evident that the species uses a wide variety of foods (Section 2.4.1), some of which in some situations may be more important to individuals than local ungulates (see Banci 1987).

Thus, habitat management for wolverines is not simple, requiring attention to the total ecosystem perhaps more than for any other species. It is beyond the scope of this report to expand on that to any great extent, other than to reiterate that reduction of wilderness "refugia" through access and alienation for timber and mineral extraction may be the greatest threat to local population viability, and to note that flooding of ungulate winter ranges for hydro development, wildfire suppression, and logging or silviculture practices that reduce biological diversity are all potentially negative for the species. In effect, successful management of wolverines requires a successful integrated management system for all the other local wildlife species on which it depends.

2.8 RECOMMENDATIONS

Unlike the case for lynx, the information presently available on life history, harvest characteristics, and user demand for the wolverine do not suggest the need for specific management changes in British Columbia. That may be either because provincial wolverine populations are secure, or because not enough is known about the species, either generally or locally, to be able to detect problems. Thus, the greatest immediate need is for better information. Following are some general recommendations for applicable activities in the near future.

To Provincial Managers

1) General: Managers should remain cognizant that scavengers such as the wolverine may be vulnerable to predator control programs involving the use of poisons (see Rausch and Pearson 1972 and Kelsall 1981).

2) Harvest Management: No specific changes in current harvest regulations are clearly required.

3) Harvest and Population Monitoring: As noted in Section 2.6.4, detection of changes in population status might best be accomplished by monitoring patterns of harvest composition as well as numbers. The recommended data gathering vehicles and activities are as follows:

- Continued compilation of wolverine harvests, by trapline, to facilitate descriptions and comparisons of harvest density and distribution at different times and in different administrative areas or ecological zones.

- Modification of the harvest data system (above) to include date of kill.

- Collection and analysis of carcass samples (skulls only) for sex and age determination, and development of a continuing baseline reporting system on harvest composition.

- Administration of an annual trapper questionnaire: Based on observations of tracks and sign, and in reference to the previous trapping season, trappers to indicate trends (increasing, decreasing, stable) for wolverine and other selected furbearers and prey species.

4) Habitat Management Habitat protection requirements and enhancement possibilities specifically for wolverine are as yet unknown, and may not exist as such. The only possible recommendation is that habitat managers continue to press for intensified consideration for all wildlife in development plans, recognizing that, for wolverines, a broadly focussed, integrated approach that promotes and protects biological diversity and richness is required, and that remote wilderness refugia play a key role in population dynamics as centers of dispersal to surrounding areas.

To Trappers

Although the wolverine is to be managed as a Class 2 species in British Columbia, with its harvest designed and administered primarily by provincial authority, intensive management at that level cannot succeed without full cooperation and support from trappers in complying with regulations and providing required samples, accurate harvest information, and conscientious responses to data gathering devices such as questionnaires. For wolverines in particular, trappers may also be able to moderate their impact on local wolverine populations, ensuring a longer term and more consistent supply, by certain voluntary actions, as follows:

- Maintain one or more "refuge" (untrapped) areas on your trapline, to serve as dispersal centers. For wolverines, such areas may simply be the rugged upland areas near or above timberline which are difficult of access in winter anyway.

- Attempt to focus on wolverine trapping in December and January, when pelts are in the most prime condition, in order to maximize returns.

- Avoid making wolverine sets near areas of very intensive use by wolverines in late winter (February or later), unless it can be ascertained that the animals involved are not denning females.

- Minimize the use of trap and snare sets that may take even the wariest animal; rather, concentrate on use of sets, particularly baited cubbies, that may take mostly young, foolish, and/or nutritionally poor animals that would be the least likely to survive anyway.

- Keep informed about habitat developments on and near traplines and, with fellow local trappers, interact with appropriate agencies to insure that furbearer values are adequately considered.

To Administrators and Researchers

Fully informed wolverine management will require more knowledge than is presently available. The relatively few intensive studies that have been undertaken to date have confirmed the difficulty of field research on the species, and further research of that kind should be directed to specific questions or problems yet to be defined. The preliminary research need in British Columbia is for a more solid description of the species distribution and abundance patterns within and between the diverse ecological zones of the province. Such a description would involve a more detailed analysis of harvest data than was possible in the present report, coupled with questionnaire information and interviews with selected trappers. Better knowledge of the nature, extent, and correlates of wolverine occurrence is prerequisite both to the identification of potentially useful research and the facilitation of appropriately responsive management.

Since trappers must be counted upon to assist in the collection of management and research information, an important focus in trapper education programs should be on the rationale and methodology for providing reliable harvest data and questionnaire responses.

* * * * *

PART 3: LITERATURE ON WOLVERINE

An Annotated Bibliography

3.1 INTRODUCTION

There have been two previous comprehensive bibliographies on *Gulo gulo*. That by Dagg and Campbell (1974a) included 287 references, with keywords, while Banci's (1982a) is an unannotated list of 607 titles. My experience in using both confirmed the need for a tighter, more selective compilation. I attempted to review most of the papers identified in the two sources cited, and found that information on wolverines was minimal in many. Indeed, in some cases the only reference to the species was a statement that it had not been seen in some particular study and/or that its local status was not known. In addition, North American interest in wolverine management is so new that the compilation deadlines in both Dagg and Campbell (1974a) and Banci (1982a), as relatively recent as they are, predate publication of the first intensive field study of the species on this continent (Hornocker and Hash 1981).

The following selected bibliography, consisting of 180 annotated references, is the basis for most of the information and ideas presented in Parts 1 and 2 of this document. Most wolverine papers are accounts of sightings and specimen records (see Section 2.1.1). The present listing generally does not include those that merely mention that wolverines were present or absent in particular areas, especially if more general sources document that fact anyway. Such "distribution" papers are included here primarily if they provided additional information on life history or relationship of the species with humans, or if they involved sightings in unusual habitats or unexpected locations. I made an exception for British Columbia material, including all formal papers encountered regardless of apparent management relevance. Unpublished records of wolverines within the species' known range were not included, even for British Columbia.

Prior to this decade, the only significant field studies on wolverine life history were conducted in the Old World, and an attempt has been made to at least identify most of those. In the time available for this compilation, I was not able to obtain copies of all such papers that my literature search suggested might be of interest, thus detailed review was not possible. Other such sources were accessible, but available only in a foreign language. If they did not have at least an English summary, and were not cited or described in other important wolverine papers, they are not included here. For the present bibliography as a whole, I am confident that I have located most of the major published and unpublished papers (particularly for North America) that relate, at least indirectly, to management of the species.

A secondary objective here was to provide sufficient information for each bibliographic entry so that the reader could A) readily understand the nature, scope, and specific conclusions relative to management, and B) confirm whether a particular paper required additional study. Annotations are generally more detailed and complete than was the case in the bibliography for lynx, both because there are so few really significant papers and because several of those are graduate theses or unpublished government reports that are not easily accessible. This section, then, is to serve both

as a summary and a "filter", hopefully reducing the need for duplication of library research effort and allowing managers more time for consideration of and action on wolverine management problems.

3.2 FORMAT

Each item in following pages consists of a complete bibliographic citation, followed by a 3-digit identification number. Most, except for a few that were not seen, also include a series of three descriptive elements, A, B, and C, defined as follows:

A) *Management Significance* - My subjective assessment of the paper's relative importance in a management context (scale of 0-3, corresponding to nil, low, medium, and high). Note that all papers on population dynamics subjects and most from British Columbia were considered to be of at least "low" (=1) significance.

B) *Geographical Location* - Broad location of study area and/or primary data source(s), usually a province, territory, state, or country, but the following designations are also given:
   a) Holarctic - study pertaining to the species' entire circumpolar range.
   b) North America - range of *G. g. luscus*.
   c) General - no particular location(s) specified.

C) *Nature and Extent of Study* - Methods, timing, sample sizes and duration.

Following the above elements are lists of keywords, under the following broad headings: Description, Habitat Characteristics, Life History, Population Dynamics, Species Management, Habitat Management, and Other Topics. Together with the identification numbers, the headings and keywords are primarily to facilitate indexing and summarization, but they also help to indicate the topical coverage of each paper. Table 14 lists and briefly defines the keywords used. That list evolved during preparation of the lynx bibliography, with the objective of its being as thorough as possible without being cumbersome, and I believe it will prove satisfactorily applicable to all furbearer management documents in this series. The overall objective was to emphasize topics with clear management implications and/or applications. The rationale for considering particular topics as "management" material is given under corresponding headings in the narrative section on considerations for wolverine management (Part 2).

The final and often longest entry under each bibliographic item, entitled "Comments", consists of statements summarizing management-related contents in detail. Again, there is a judgemental aspect to material included--I have attempted to err on the side of completeness. While I have often paraphrased and summarized, I have attempted to be faithful to each author's material and interpretations, and have neither evaluated nor critiqued.

TABLE 14. WOLVERINE BIBLIOGRAPHY: SUBJECT HEADINGS AND KEYWORDS.

DESCRIPTION
- features (physical form, size, variations)
- taxonomy
- distribution (including "unusual" occurrences)

HABITAT CHARACTERISTICS
- study/area (general description)
- vegetation (broad habitat classifications)
- cover (vegetation types as related to particular activities)
- climate (seasons, temperature, precipitation as factors relevant to populations).

LIFE HISTORY
- lifehist (general, covering all or most aspects)
- food (food habits, broad or seasonal)
- nutrition (aspects of metabolism and growth)
- activity (daily and/or seasonal patterns)
- hmrange (home range)
- movements (daily and/or short term)
- dispersal (including immigration and emigration)
- socbehav (social behavior, territoriality)
- behavior (other than social behavior, e.g. foraging)
- health (condition, parasites, diseases)
- denning (characteristics/use of dens, beds, nests)
- pelage (fur characteristics, moult patterns, pelt primeness)

POPULATION DYNAMICS
- cycles (periodic population fluctuations)
- natality (fecundity, productivity, reproductive biology)
- mortality (documentation of causes and/or rates)
- poptrend (population numbers, densities, indices)
- popcomp (sex and/or age composition)
- popreg (population regulation, limiting factors)

SPECIES MANAGEMENT
- census (methods for assessing numbers, trends, indices)
- age/tech (determination of specimen ages)
- gen/tech (field study methods, including capture, handling, marking, telemetry)
- kill/tech (methods of collecting and analysing harvest data)
- repro (methods of assessing productivity, from specimens)
- economics (fur and/or ecological value, depredations)
- harvest (nature, extent, and/or effects)
- interactions (relationships with other species)
- harv/strategy (harvest options, recommendations, regulations)
- transplants (introductions to new or formerly occupied range)
- refuges (parks, management areas)

HABITAT MANAGEMENT
- fire (effects of wildfire and associated succession)
- other/nat (effects of other natural forces--e.g., flood, insect damage).
- forestry (effects of logging and silvicultural treatments, and associated succession).
- other/impacts (effects of human developments other than forestry: agricultural alienation, access, dams...)
- hab/strategy (recommendations, prescriptions)

OTHER TOPICS - mostly little or no perceived direct significance for management, e.g., history, bibliography, paleontology, zoogeography, physiology, morphology, genetics, evolution, embryology.

* * * *

3.3 WOLVERINE BIBLIOGRAPHY

Addison, E.M., and B. Boles. 1978. Helminth parasites of the wolverine *Gulo gulo* from the District of Mackenzie, Northwest Territories, Canada. Can. J. Zool. 56:2241-2242.

001 A) 1; B) Northwest Territories; C) Examination of digestive tracts and other tissues from 39 trapped specimens.
Life History - health.
Comments - Helminths were found in 38 of the 39 digestive tracts examined (3 species of cestodes, 2 nematodes, and 1 trematode), but there were apparently no negative population or individual condition implications of the parasite incidence observed; none of the diaphragms examined (38) contained larval *Trichinella*.

B.C. Hydro. 1981. British Columbia Hydro and Power Authority, Registered Trapline Program. 24pp.

002 A) 1; B) British Columbia; C) Considerations for compensating trappers whose traplines are affected by hydro developments.
Species Management - harv/strategy.
Habitat Management - other/impacts, hab/strategy.
Comments - Supporting data and habitat definitions are not given in this document, but "reasonable harvest densities" (number of wolverines/km^2) in poor, moderate, and good habitats, respectively, are listed at 0.0015, 0.003, and 0.0075; in reference to three "life styles", aquatic, seral, and climax, wolverines are relegated to the last.

Bailey, T.N. 1981. Factors influencing furbearer populations and harvest on the Kenai National Moose Range, Alaska. Pages 249-272 *in* J.A. Chapman and D. Pursley (eds). Worldwide furbearer conference proceedings, Aug. 3-11, 1980, Frostburg, Maryland.

003 A) 1; B) Alaska; C) Review of furbearer and harvest data on the refuge.
Population Dynamics - poptrend.
Species Management - harvest.
Habitat Management - fire.
Comments - It is speculated that "since prime habitat of wolverines on the refuge appears to be along the more rugged mountainous forest edges and alpine areas, fires probably have not significantly influenced wolverine habitat"; initial impact on prey species might be detrimental, but wildfire effects on food supply would probably be beneficial in the long term.

Ballard, W.B., A.W. Franzmann, and C.L. Gardner. 1982. Comparison and assessment of drugs used to immobilize Alaskan gray wolves (*Canis lupus*) and wolverines (*Gulo gulo*) from a helicopter. J. Wildl. Dis. 18:339-342.

004 A) 2; B) Alaska; C) Monitoring of results during field use.
Species Management - gen/tech.
Comments - Etorphine is favored for use on these two species because it enables quick recovery and therefore does not expose animals to prolonged exposure to extreme temperatures or accidents; a dosage of 0.7 mg etorphine mixed with 50 mg of xylazine is recommended for aerial darting of wolverines weighing 10.5 - 17.7 kg.

Banci, V.A. 1982a. A bibliography on the wolverine *Gulo gulo*. Research, Ministries of Environment and Forests. IWIFR-9. Victoria. 53pp.

005 A) 2; B) General; C) Literature search and compilation of references.
Other Topics - bibliography.
Comments - This is the most complete of the wolverine bibliographies in terms of number of titles (607), although the treatment of the species in a large proportion of that total is little more than a mention of the name; further, it consists only of a simple list, without annotations or topic headings, making it less useful than it otherwise might be.

Banci, V.A. 1982b. The wolverine in British Columbia: distribution, methods of determining age and status of *Gulo gulo vancouverensis*. Research, Ministries of Environment and Forests. IWIFR-15. Victoria. 90pp.

006 A) 2; B) British Columbia; C) Literature review and examination of museum specimens.
Description - taxonomy, distribution.
Species Management - age/tech.
Comments - A comparison of skull features and dimensions leads to the conclusion that the Vancouver Island wolverine is not sufficiently different to warrant a separate subspecies status; age determination in wolverines is difficult because the species grows and matures quickly-- there were no significant correlations with age among several combinations of cranial and dental measurements; an "enamel line" technique was evaluated and found of little use for the species; annuli are present in dental cementum, but teeth are difficult to prepare, resulting sections are difficult to read, and there is little known age material to correlate annuli numbers and age; further, wolverines may show more variable cementum deposition patterns than most species because they experience less pronounced seasonal nutritional differences (food is often most available to them in winter) and/or because there may be more variation in nutritional patterns between years; for those reasons, and because juveniles and subadults are difficult to separate by the method in any event, cementum annuli analysis may not be appropriate for wolverine--preliminary results with a technique involving measurement of the canine pulp cavity have been promising; a provincial distribution map, compiled from literature records, anecdotal accounts, and harvest records show that the species occurs throughout B.C., but probably most significantly in the

northern half, although observations and records anywhere along the coast are rare; the need for information on habitat requirements and population characteristics in the province is emphasized.

Banci, V.A. 1987. Ecology and behavior of wolverine in Yukon. Unpubl. M.Sc. Thesis, Univ. British Columbia, Vancouver. 178pp.

007 A) 3; B) Yukon Territory; C) Field studies with telemetry and laboratory study of 461 trapped specimens, 1982-1985.
Description - features, distribution.
Habitat Characteristics - study area, cover, climate.
Life History - food, hmrange, movements, dispersal, socbehav, behavior, health.
Population Dynamics - natality, mortality, poptrend, popcomp, popreg.
Species Management - age/tech, kill/tech, repro, harvest, harv/strategy, interactions.
Comments - This study represents the most thorough and wide-ranging field study of the species that has been undertaken in Canada, and since there has as yet been no formal publication of results in easily obtainable sources, detailed coverage is provided here; **REPRODUCTION** - among 180 usable female samples, 109 (61%) were in the first two age classes, with all of 82 kits (age 0+) and 25 of 27 subadults (1+) in the "non-reproductive" category; for the 71 older animals, those found to be in the reproductive (pregnant or post-partum) group included 16 of 30 in age 2+, 12 of 13 in each of 3+ and 4+, 6 of 7 in age 5+, and only 3 of 8 in a combined 6+ - 11+ group; overall, owing partly to the young age distribution of the sample, only 53 of 180 females in the sample (29.4%) were in the reproductive class; the mean *in utero* litter size was 3.2, and there was evidence for litter size increasing with age of female, ranging from 2.8 to 3.4 in ages 2+ to 5+; it is emphasized that the laboratory results, though indicating low productivity, probably are nevertheless optimistic because they fail to account for intra-uterine and pre-weaning losses; implantation occurred as early as November and some births as late as March, but there was some evidence that most parturition may be in February; males were sexually mature at 2+ years, and showed some evidence of increased breeding condition by late winter (March); **AGE DETERMINATION** is a problem for this species--though not considered ideal, dental cementum analysis using upper premolars was used in this study; **FEATURES (SIZE)** - adult males were heavier than younger animals, but body measurements did not differ--estimated whole weights for kits, subadults, and adults, respectively, were 11.5 kg (n=59), 11.9 kg (n=44), and 12.8 kg (n=111); comparable weights for females were 8.3 kg (n=60), 7.9 kg (n=30), and 8.7 kg (n=82)--the lower figures for subadult females was possibly due to weight loss during their initial period of independence (a year later than for males); the largest estimated weights were 14.4 kg (female) and 21.3 kg (male); whole weights of live-trapped males varied from 10.2 kg for a kit to 15.0 kg for an adult aged 10+, and averaged 13.0 (n=5)--comparable figures for females were 6.6 and 7.8 kg for two kits, up to 11.0 kg for an adult, with a mean of 8.7 kg (n=5); **CONDITION** - a kidney fat index and a visual estimate of total body fat were both considered inadequate for measuring condition, although there was some evidence that females were in low in body fat more often than males; **FOOD HABITS** - detailed

comparisons of stomach contents for quick-killed and restrained animals indicated that consumption of trap bait was rare and unlikely to bias food habits results; based on 411 stomach, 95 (23.1%) were empty-- suggesting that food was generally difficult to obtain; frequency of occurrence and percent dry weight of major prey items in the remaining 316 stomachs was snowshoe hare (18.5, 6.7), porcupine (10.9, 0.8), moose (9.7, 12.5), caribou (5.4, 8.0), red squirrel (4.4, 0.7), and ground squirrel (2.4, 0.9); flesh, fat, and bone not identified to specific groups, but believed mostly from wild ungulates, had a combined frequency of 32.9% and a percent dry weight occurrence of 31.0--that category combined with the identified ungulate remains demonstrates its major importance in the diet (believed mostly scavenged); other ungulates identified (besides moose and caribou) were elk, mule deer, thinhorn sheep, and mountain goat, all at occurrences and dry weight percentages of 2% or less; other prey remains, all at low incidence, were shrew, pika, chipmunk, flying squirrel, marmot, beaver, at least 4 species of microtines, traces of marten, mink, weasel, coyote, wolf, lynx, unident. fish, and birds from at least 4 families; the greatest diet variability in the sample period was in November, when snow cover is usually least; the hibernators among the small mammal prey were believed taken from caches; small mammals were rarely found in the same stomachs with ungulates, suggesting that they were hunted when larger items were not available; snowshoe hare occurrence (the most frequent identified item) was despite the fact that the study commenced during the year of the species' cyclic decline; other evidence of food use included observations of wolverines carrying or chasing ground squirrels, tracks indicating hunting of ptarmigan, use of spawned salmon frozen into river ice, and use of garbage at a camp; in addition, 5 of 12 winter scats contained kinnikinnick berries; **HOME RANGE** - 10 wolverines were radio-collared, but only 5 (3 adult females, 1 adult male, and 1 subadult male) were monitored significantly; all 3 adult females made long distance "excursions" in summer, but without those (whose purpose was not determined), summer and winter ranges were similar in size; only 1 of the 3 females produced young, and her annual home range (139 km^2) was half that of the two without kits (202 and 343 km^2); the adult male's range (238 km^2) was only slightly larger than the average for the females and was much smaller than that of the juvenile male (526 km^2), whose movements suggested dispersal; animals sometimes remained in relatively small areas for long periods, presumably because a large food supply (perhaps one or more ungulate carcasses) was available in that area--range size appears generally related to food availability for both sexes, although access to females may also be a factor for males; **MOVEMENTS** - daily movements were generally small, averaging less than 1.5 km/day for most individuals--the longest single daily movement recorded was 17.3 km, by a male kit; **MORTALITIES** among collared animals included a) a subadult male and an old (age 10+) male, both trapped (outside the study area?), b) a male kit apparently killed by wolves, c) an old adult female that first sustained an injury (believed by a wolf), and after being recaptured 3 times in the month following, died in captivity--autopsy showed "parasitic pneumonia" and a kidney disease, d) a female kit believed to have starved, and e) another female kit whose cause of death was "...suspected to be starvation and/or injury"; the energetic demands of producing and feeding young are emphasized as a major potential factor in the condition and survival of females--the one that eventually died in captivity was suspected to have been "weakened" initially in that way; reference is also

made to an apparent wolf kill of an uncollared adult male; **HABITAT** use did not differ from availability for females, either generally or seasonally; both collared males used subalpine conifer habitat more in winter and alpine talus less in summer than expected based on availability; there were individual variations, but when data were combined by sex, there were no significant patterns of use of different aspects, elevations, or percent forest cover types; **TERRITORIALITY** - little information on range overlap between and among sexes was obtained although scent-marking, especially by residents, was recorded; **HARVEST** - in regard to harvest patterns, it is acknowledged that climate and economic factors, which may vary from year to year, influence trapper activity; the sex ratio of the harvest varied from 1:1 significantly in only 1 of the 3 study years, but was significant at 1.3:1 in favor of males for the overall sample 258:204; age ratios were not different within sexes or among years, the total harvest comprising 213 juveniles and 200 adults (2+ and older); male kits showed the earliest vulnerability, as the class caught most often in November-January in all years (peak in January); subadult males had a harvest peak in February, possibly their dispersal time; subadults were the smallest harvest class; female kits appear to establish ranges in their natal areas and were apparently not particularly vulnerable until later in the winter (a pattern similar to that for adult males); adult female harvest peaked in February, possibly as they became more mobile and vulnerable to meet the nutritional requirements for parturition and lactation; **NUMBERS** - based on population indices developed for trapped ecoregions, and an estimated density of 1 resident per 177 km^2, the total Yukon wolverine population was estimated at about 4380 animals; **GENERAL CONCLUSIONS** - availability of food is considered a major factor mediating range size, movements, possibly timing of parturition, reproductive success, and survival of young--vagaries of climate and its seasonal effect on large ungulates is one of several complicating factors; bad winters for ungulates are probably good for wolverines; "As food resources are not consistent among areas nor over time, patterns of habitat use are expected to vary seasonally and locally."; no single habitat type can be identified as important for the species, but large areas providing a diversity of habitats are believed to be required; **HARVEST STRATEGY AND RECOMMENDATIONS** - differential vulnerability of sex and age classes may offer some opportunity for harvest control, although the actual vulnerability pattern of females is still unclear; it is suggested that during winters when availability of food is low, reproduction may be affected and harvest pressure should be reduced; finally, it is recommended that the species status as "big game" should be changed and hunting (which accounts for about 10% of the annual harvest) stopped, since it probably does not act on normal vulnerability patterns, and usually takes animals when pelts are inferior.

Bandy, P.J. 1952. A study of the furbearing mammals of the subalpine and Columbia forest regions of British Columbia in relation to fur production from 1929 to 1949. Unpubl. B.A. Thesis, Univ. British Columbia, Vancouver. 82pp.

008 A) 1; B) British Columbia; C) Interpretation of furbearer distribution, abundance and population trends from trapper harvest data.
Description - distribution.
Population Dynamics - poptrend.
Species Management - harvest.
Comments - For the Subalpine and Columbia forests of central and southeastern B.C., wolverine numbers were thought to be declining in the late 1940's as compared to the early 1930's (larger area per harvested animal, despite increased overall harvests), with trapping implicated as a cause; harvest densities indicated for 1929-33, 1934-38, 1939-43, and 1944-49, respectively, were about 7425, 4100, 4600, and 5625 km^2/pelt.

Banfield, A.W.F. 1974. The mammals of Canada. U. of Toronto Press, Toronto. 438pp.

009 A) 0; B) Canada; C) Literature review.
Description - features, distribution.
Life History - lifehist.
Comments - This is mostly a summary of "existing knowledge", although with a short bibliography; it is stated that wolverines have a taste for porcupines, but that "...a few of them have succumbed later because of the piercing of the stomach by the undigested quills"; the Canadian center of abundance is said to be the tundra zone of the Yukon and Northwest Territories, and that "in recent years hunters and trappers have greatly reduced its numbers."

Bangs, E.E., and T.N. Bailey. 1987. Furbearer and trapper management on the Kenai National Wildlife Refuge, Alaska. Page 19 (abstract only) *in* Townsend, B. (ed). Abstracts of the Fourth Northern Furbearer Conference, 3-4 April 1987, Alaska Dep. Fish and Game, Juneau, Alaska.

010 A) 1; B) Alaska; C) Monitoring of trapping effort and harvest.
Species Management - harvest, harv/strategy.
Comments - The wolverine is one of 4 species that are believed to have been impacted by heavy trapping pressure and "high harvest levels" on the refuge (others are lynx, wolf, and beaver).

Barker, M.S., Jr., and T.L. Best. 1976. The wolverine *Gulo luscus* in Nevada. Southwest. Nat. 21:133.

011 A) 0; B) Nevada; C) Report of a specimen record.
Description - distribution.
Comments - The first record of the species in Nevada, based on the finding of skeletal materials in a cave where the animal (and representatives of other species) had apparently fallen; includes cranial measurements.

Bee, J.W., and E.R. Hall. 1956. Mammals of northern Alaska. Univ. Kansas Mus. Nat. Hist, Misc. Publ. No. 8.

012 A) 1; B) Alaska; C) Compilation of specimen and sight records.
Description - distribution.
Life History - food, behavior.
Comments - In arctic Alaska, the wolverine is scarce along the coast, but is more abundant in uplands of the "Plateau Province" and the Brooks Range; caribou carrion, both as provided by wolf kills and by deaths from "natural causes", is given as the chief source of food; it is considered likely that "all kinds of small rodents" are used, but it has been observed digging only for ground squirrels and singing voles; of 20 observations, 1 involved 3 animals, 2 were in pairs, and 17 were of singles, confirming the species generally solitary nature.

Beidleman, R.G. 1956. An early record of the wolverine in western Nebraska. J. Mammal. 37:445-446.

013 A) 0; B) Nebraska; C) Literature review.
Description - distribution.
Comments - past occurrence of the wolverine in western Nebraska is documented with accounts of a sight record in 1837, "several" sight records from the 1880's, and a specimen obtained in 1887.

Biese, W. 1936. Das geologische alter der vielfrassreste. (Geological age of glutton remains). Zeitschr. Saugetierk. 11:319-320.

014 A) 0; B) Europe; C) Incidental field observations.
Other Topics - history, paleontology.
Comments - All in German--not translated; photos and diagrams show location of wolverine remains in deep caves, possibly entrapment areas such as described in Barker and Best (1976).

Birney, E.C. 1974. Twentieth century records of wolverine in Minnesota. Loon 46:78-81.

015 A) 1; B) Minnesota; C) Evaluation of sight and specimen records.
Description - distribution.
Comments - None of several records for this century were sufficiently documented so that they could be confirmed; the previously most convincing record, involving a wolverine ostensibly shot in St. Louis County in 1967, was found to have been a hoax (the animal apparently having actually been brought back from a Canadian hunting trip); it is concluded that the last unequivocal record for the state was in 1899, and that probably the only wolverines that have set foot in the state since that time (if any) have been occasional wanderers from Canada.

Boles, B.K. 1977. Predation by wolves on wolverines. Can. Field-Nat. 91:68-69.

016 A) 2; B) Northwest Territories; C) Incidental field observations.
Life History - food, behavior, health.
Species Management - interactions.
Comments - Two wolverines were killed by wolves--a young female (age 2) in a trap was observed being killed by a single wolf (19 Jan. 1974), and an old male (age 14-15) was apparently killed by about 4 wolves (tracks in snow, 20 Nov. 1974); the female's heart was apparently eaten but otherwise both were left relatively intact, thus it is not clear if they were killed as prey; both animals were in relatively good condition, as measured by a "kidney fat index"--female 30.4% and male 20.8% in comparison to a general sample of winter caught males (17.8% , n=20) and females (18.5%, n=19); Alaskan naturalist A. Murie is cited as having observed three unsuccessful attacks of wolves on wolverines, with the wolverines escaping by climbing trees in each case; the dead male's stomach contained ptarmigan; porcupine quills were found in only 1 of 54 wolverine carcasses studied (most probably not including the hide).

Bulmer, M.G. 1974. A statistical analysis of the 10-year cycle in Canada. J. Animal Ecol. 43:701-718.

017 A) 1; B) Northwest Territories; C) Statistical analysis of historic and recent harvest data.
Population Dynamics - cycles.
Comments - This paper confirms, mathematically, the existence and nature of the 10-year cycle, particularly as exemplified by the lynx; the data are said to indicate that the wolverine was cyclic both in the last half of the 19th century and in the period 1920-1965, following lynx by 3-4 years and, like that species, probably in response to hare abundance.

Bulmer, M.G. 1975. Phase relations in the ten-year cycle. J. Animal Ecol. 44:611-620.

018 A) 0; B) General; C) Literature review/mathematical analysis.
Population Dynamics - cycles.
Comments - The author claims that snowshoe hares are "dominant items" in the food of several furbearers, including wolverine, and interprets changes in historical fur harvests of those species to be delayed responses to hare declines; in the case of the wolverine, a "phase lag" of 4 years is observed, and it is concluded that "...delayed implantation has delayed the cycle by a year....shortage of food acts either on the number of ova shed or on the proportion of females which mate at age 1"; as an alternative, it is suggested that the wolverine, as a "well known scavenger" is more likely to be trapped when hares are scarce, and that "...the cycle in this species is an artefact due to trapping factors."

Burkholder, B.L. 1962. Observations concerning wolverine. J. Mammal. 43:263-264.

019 A) 1; B) Alaska; C) Incidental field observations.
Life History - food, behavior.
Population Dynamics - mortality.

Species Management - interactions.
Comments - Two observations are reported, the first involving an adult caribou being attacked, and eventually killed by a wolverine (mid- January 1953), and the second a record of a small female wolverine being killed by wolves when caught in the open at a kill site--an apparent attempt to escape by climbing a willow failed; the wolverine was eviscerated, but no part of it was eaten; none of the 8 wolves involved, seen the next day, appeared to have been injured in the encounter.

Buskirk, S.W., P.F.A. Maderson, and R.M. O'Connor. 1986. Plantar glands in North American Mustelidae. Pages 617-622 *in* D. Duvall, D. Muller-Schwarze, and R.M. Silverstein (eds). Chemical signals in vertebrates 4. Plenum Press, New York.

020 A) 1; B) General; C) Laboratory examination of several Mustelid species.
Life History - socbehav.
Other Topics - morphology.
Comments - Structures provisionally identified as glands are found on the plantar pads of the rear feet of marten, fisher, river otter, and wolverine, but not in several other species; it is speculated that the glands function in passive chemical communication, enabling these wide- ranging species to "broadcast" their presence extensively by normal location, on objects contacted by the hind feet, without the need to engage in energy expending behaviors.

Cahn, A.R. 1937. Mammals of the Quetico Provincial Park of Ontario. J. Mammal. 18:19-29.

021 A) 0; B) Ontario; C) Compilation of anecdotes.
Description - distribution.
Population Dynamics - poptrend.
Other Topics - history.
Comments - Wolverines were formerly present, but trappers are cited as saying that it had been extirpated by about 1900.

Carl, G.C., and G.A. Hardy. 1944. Flora and fauna of the Paradise Mine area British Columbia. Pages C18-C38 *in* Rep. Prov. Mus. Nat. Hist. and Anthro., 1944. Victoria.

022 A) 1; B) British Columbia; C) Anecdotal information.
Description - distribution.
Comments - A wolverine was one of the species reported seen in the mine area (Purcell Mountains, near Windermere).

Casey, T.M., P.C. Withers, and K.K. Casey. 1979. Metabolic and respiratory responses of Arctic animals to ambient temperature during the summer. Comp. Biochem. Physiol. 64A:331-342.

023 A) 0; B) Alaska; C) Metabolic studies of captive animals.
Other Topics - physiology.

Comments - Summer acclimatized arctic mammals displayed respiratory performances similar to those of temperate mammals; differences in body mass and summer versus winter pelage are featured in comparisons, but no management implications are apparent.

Clarke, C.H.D. 1944. Notes on the status and distribution of certain mammals and birds in the Mackenzie River and Western Arctic area in 1942 and 1943. Can. Field-Nat. 58:97-99.

024 A) 1; B) Northwest Territories; C) Incidental field observations and interview information.
Description - distribution.
Species Management - economics.
Comments - The species occurs regularly, but not in abundance, along the Mackenzie and in the barren lands, and "...in the mountains west of Aklavik they may even by common"; the demand for wolverine skins is great among local Eskimos, and most of the skins obtained at Aklavik and Tuktoyaktuk are reportedly imported "...chiefly from British Columbia."

Cockerton, D., and S. Herrero. 1973. A study of wolverine home range and behavior by tracking. Unpubl. Rep., Mt. Assiniboine Prov. Park, British Columbia. 23pp.

025 A) 1; B) British Columbia; C) Snow-tracking.
Life History - hmrange, movements.
Not seen: cited and some findings presented in Holbrow (1976).

Coues, E. 1877. Fur-bearing animals: a monograph of North American Mustelidae. Dept. Interior, U.S.G.S. Misc. Publ. No. 8, Washington, D.C. 348pp.

026 A) 0; B) North America; C) Study of museum specimens; review of literature and anecdotes.
Description - features, distribution, taxonomy.
Life History - lifehist.
Comments - One of the earliest detailed accounts of the species, particularly for this continent, the chapter on wolverine provides details of description and taxonomic history, aspects of life history as then understood, and considerable elaboration on behavior (with several anecdotes of interactions with humans); its distribution is described as circumpolar, existing in the north even on some of the Arctic Islands (e.g., Melville Island), and southward to about 42° N in the east and possibly to 39° N in the west (southern Rockies); as in present times, the areas of greatest abundance were in the north, e.g. the Mackenzie River region; it is noted that some observers report the wolverine as easy to trap (its "...perpetual greed...completely overbalances its caution..."), however many other reports and anecdotes indicate that at least some individuals do not fit that description.

Cowan, I.McT. 1936. Notes on some mammals in the British Columbia Provincial Museum with a list of the type specimens of North American recent mammals in the museum. Can. Field-Nat. 50:145-148.

027 A)1; B) British Columbia; C) Review of museum collection data and examination of specimens.
Description - features, taxonomy, distribution.
Comments - The wolverine section features the Vancouver Island race; the two specimens available are described and compared to others from the adjacent mainland coast (Bella Coola), and from northwestern B.C. (Telegraph Creek); includes cranial measurements for 5 specimens.

Cowan, I.McT. 1938. The fur trade and the fur cycle: 1825-1857. British Columbia Hist. Quart. 2:19-30.

028 A) 1; B) British Columbia; C) Analysis of fur returns.
Population Dynamics - cycles, poptrend.
Species Management - harvest.
Other Topics - history.
Comments - Examining historic B.C. fur returns for trends in species occurrence and abundance, the author noted that although wolverines doubtless consume large numbers of hares during peak years, "...no relation can be traced between fluctuations in their numbers and the rabbit cycle."

Cowan, I.McT., and C.J. Guiguet. 1965. The mammals of British Columbia. B.C. Prov. Mus. Handbook No. 11, Victoria. 414pp.

029 A) 1; B) British Columbia; C) Literature review; compilation of specimen records.
Description - features, distribution.
Habitat Characteristics - vegetation.
Life History - lifehist.
Comments - "The wolverine is a creature of the northern wilderness frequenting wooded and mountainous areas"; in summer it commonly forages near timberline and on talus slopes; the distribution is given as "throughout the province in the mountainous areas..."--although uncommon on the coast proper, it is found in the high mountains of the Coast Range; two females from Vancouver Island weighed 8.8 and 6.7 kg, respectively.

Cunningham, J.D. 1959. The wolverine and the fisher in the Yosemite region. J. Mammal. 40:614-615.

030 A) 0; B) California; C) Compilation of sight records.
Description - distribution.
Comments - An account of 5 different sightings, one involving 2 animals, in the period 1951-53 (all summer records); some previously unreported historical records (1929-1941) are also given.

Dagg, A.I., and C.A. Campbell. 1974a. An annotated bibliography on the status and ecology of the wolverine in Canada. Can. Wildl. Serv. Manuscript Rep., Ottawa. 45pp.

031 A) 1; B) Canada; C) Literature search and compilation of references.
Population Dynamics - poptrend.
Species Management - harvest.
Other Topics - bibliography.
Comments - It is noted that although the wolverine is largely a Canadian species in North America, it was featured in only 1 "...of 639 articles...on Canadian mammals published over the past 40 years in 14 well-known refereed journals or series..."; the bibliography lists 287 articles, complete with keywords for a variety of biology and management subjects, and including general mammal distribution papers that mention wolverine only briefly or, in some cases, not at all (the negative information apparently considered significant in those cases); only 17 of the listed papers were considered "very useful", and just 6 of those based on observations in North America; appendices include provincial, territorial, and Canada-wide pelt sales for the period 1921-1972, summaries of species status by province and territory, and a summary of museum specimen holdings.

Dagg, A.I., and C.A. Campbell. 1974b. Historic changes in the distribution and numbers of wolverine in Canada and the northern United States. Unpubl. Rep., Can. Wildl. Serv., Ottawa. 21pp.

032 A) 2; B) Canada; U.S.A.; C) Literature review.
Description - distribution.
Population Dynamics - poptrend, popcomp.
Species Management - harv/strategy.
Other Topics - history.
Comments - It is believed that "...the wolverine is one of the rarest mammals in Canada, especially in the east", but there is little specific data on its exact distribution and abundance; there are differences of opinion as to whether the species occurs primarily in taiga, tundra, or the transition zone habitat along the treeline, but there appears to be evidence that it formerly occurred farther southward, into broadleaf forest, in both North America and Europe; prehistorically the wolverine occurred in most Canadian provinces, but has apparently always been absent from most islands south of the arctic circle on both coasts--Nova Scotia, Prince Edward Island, Newfoundland, Anticosti Island, Queen Charlottes--(but present on Vancouver Island); the species was apparently extinct in New Brunswick by about 1850, and its range has shrunk to the extreme north in Quebec, Ontario, Manitoba, Saskatchewan, and Alberta--the geographic range in B.C., Yukon, and N.W.T. is considered to have remained about as in historic times, with possible increases in some of the arctic islands which are reached by ice crossings; in the U.S., wolverines were recorded and possibly resident in at least 22 of the 48 contiguous states, but their range has now shrunk to a small nucleus population in seven western states; estimates of relative numbers, based on harvests and subjective reports, suggest declines in most areas; possible causes listed for the postulated declines are over-trapping and hunting, habitat changes, intolerance to human developments, poisoning during predator control operations, the

decline of caribou, reproductive failure due to imbalanced sex ratio and/or reduced numbers, and negative effects of the changing (warming) climate; recommendations for management include hunting and trapping closures in eastern Canada, more intensive harvest monitoring in northern and western Canada, establishment of special parks and/or reserves, transplants, increased public education, captive breeding, and increased research.

Danilov, N.D. 1965. Some data on the reproduction of glutton. Zool. Zhurnal 44:1737-1739. (Engl. Translation 1117, Foreign Languages Div., Dept. Sec. State, Ottawa. 5pp.)

033 A) 0; B) USSR; C) Laboratory examination of 2 animals, 1 of each sex.
Population Dynamics - natality.
Comments - Much description and several measurements, but no new knowledge; both specimens were taken in about mid-March, and it was concluded that the male was sexually active and the female in "pro- estrous" at that time.

Davis, D.G. 1967. A brief note on the birth of wolverines. Internatl. Zoo Yearbook 7:127.

034 A) 1; B) Montana; C) Observation of captive animals.
Life History - nutrition, behavior, pelage.
Population Dynamics - natality.
Comments - Two young were born at the zoo on 16 February 1965--mating was not observed, so the length of gestation was not known; the young, which were "pure white" at birth, did not emerge from the den until late April, and then only at night; they first came out in daylight in mid- May, at age 3 months, and by that time were in pelage resembling that of the adults.

De Vos, A. 1964. Range changes of mammals in the Great Lakes region. Amer. Midland Nat. 71:210-231.

035 A) 0; B) Canada, U.S.A.; C) Literature review.
Description - distribution.
Comments - The wolverine is thought to have had a wide range throughout the Great Lakes region (Minnesota, Michigan, Wisconsin, south and central Ontario, Ohio, Pennsylvania, and New York) prior to arrival of the white man, though in only small numbers, but has been essentially extinct in that area since the early part of the present century.

Dice, L.R. 1921. Notes on some mammals of interior Alaska. J. Mammal. 2:20-31.

036 A) 0; B) Alaska; C) Review of literature and anecdotes.
Description - distribution.
Comments - Wolverines were considered "rare or absent" over most of interior Alaska (no significant details).

Dixon, J. 1925. Closed season needed for fisher, marten, and wolverine in California. Calif. Fish and Game 11:23-25.

037 A) 1; B) California; C) Consideration of fur harvest data.
Population Dynamics - poptrend
Species Management - harvest, harv/strategy.
Comments - Reduced harvests of the three species named (1920-24) were thought to have reflected population declines, and a three-year closed season was recommended; in the case of wolverines, the harvest numbers involved over the five-year period were 2,2,1,3, and 0.

Dunn, E.J., and E.A. Stanlake. 1978. The family Mustelidae: a bibliography. Fish and Wildl. Bull. No. B-4, British Columbia Wildlife Branch, Victoria. 73pp.

038 A) 1; B) General; C) Literature search and compilation of mustelid references, primarily as listed in Wildlife Review, 1960-1978.
Other Topics - bibliography.
Comments - The wolverine section comprises 66 references, including 51 listed previously in Dagg and Campbell (1974a), 4 apparently missed by those authors, and 11 new publications (1974-77).

Edwards, R.Y., and I.McT. Cowan. 1957. Fur production of the boreal forest region of British Columbia. J. Wildl. Manage. 21:257-267.

039 A) 1; B) British Columbia; C) Analysis of harvest records, 1929-1948.
Description - distribution.
Habitat Characteristics - vegetation.
Population Dynamics - poptrend.
Species Management - harvest.
Comments - The wolverine is trapped intensively both because its fur is in demand and because it has a reputation for destructiveness on the trapline, thus it is believed that fur yields closely reflect population density; among 7 boreal forest subregions in northern B.C., the highest production of wolverines is on the "high, cold plateaux in the northwest" (Yukon Forest - 600 km^2 per pelt, Stikine Forest, 900 km^2 per pelt), followed by somewhat lower production in the Liard Forest (1090 km^2 per pelt), and with the lowest production in lowlands along the Alberta border (Nelson Forest, Northern Peace Forest, Peace Parkland, and Southern Peace Forest, 1790 - 23,650 km^2 per pelt); wolverine production was generally highest near mountains, even within the area of generally lowest production in the northeast.

Erlinge, S. 1986. Specialists and generalists among the mustelids. Lutra 29:5-11.

040 A) 1; B) General; C) Literature review.
Habitat Characteristics - vegetation.
Life History - nutrition, behavior.
Population Dynamics - natality, poptrend.

Comments - Wolverines are characterized as large mustelids that use a variety of foods (i.e., are generalists) and occupy forest and tundra habitats; large mustelids generally have low natality (delayed sexual maturity and small litter size), but lower mortality rates and therefore more stable populations than smaller mustelids; generalists, using a variety of food sources, are less affected by fluctuations in particular prey populations or by environmental changes; however, large mustelids require large areas of suitable habitat to sustain viable populations.

Ewer, R.F. 1973. The Carnivores. Cornell Univ. Press, Ithaca, New York. 494pp.

041 A) 1; B) General; C) Literature review.
Description - features.
Life History - food, behavior, denning.
Population Dynamics - natality.
Other Topics - genetics.
Comments - The wolverine is described as "...rather like an over-grown marten"; no original material is presented, but this reference is of interest in providing a translation of several conclusions from Krott (1959a), the source of all following points; the wolverine's year is divided into essentially two seasons--that with snow and that without; carrion and cached food dominates in the winter diet, while small rodents, bird's eggs, wasp nests, and berries are commonly taken in summer; food remaining after a meal is cached, and is important to survival in times when hunting is difficult--ability to locate caches is not limited to ones they made themselves, so raiding of others stores (including those of man) is common; the anal gland secretion is emitted only when the animal is alarmed, while the ventral gland is used for marking; female territories are included within those of males, but are usually exclusive from each other--the size of the territory is believed related both to availability of food and of den sites; wolverines are believed to provide "prolonged post-weaning maternal care" and to breed only every other year; the species diploid chromosome number is given as 42 (the same as the least weasel and 4 more than martens and fishers).

Filinov, C. 1980. Predator prey problems in nature reserves of the European part of the Russian U.S.S.R. J. Wildl. Manage. 44:389-396.

042 A) 0; B) USSR; C) Long-term field investigations.
Population Dynamics - poptrend.
Species Management - economics.
Comments - Wolverines were listed present in only 2 of 9 nature reserves studied, and those were also the only two reserves supporting reindeer; the estimated densities (km^2/wolverine) for those two reserves, Laplandsky and Pechoro-Ilychsky, were 135-160 (10-12 animals) and 290-360 (20-25 animals), respectively; wolverine predation accounted for 2.4% of all documented natural mortality of moose and 10.2% of natural mortality for reindeer at Laplandsky; comparable figures for Pechoro- Ilychsky were 5% (moose) and 51% (reindeer); wolverine hunted reindeer more than they did other ungulates; it was concluded that predation was not a significant factor for the ungulate populations involved.

Flook, D.R., and J. Rimmer. 1965. Cannibalism in starving wolverines and sex identification from skulls. Can. Field-Nat. 79:171-173.

043 A) 1; B) Alberta; C) Observations at an abandoned water tank that had become a mammal trap.
Life History - nutrition, behavior.
Population Dynamics - popcomp.
Species Management - gen/tech.
Comments - A total of 5 wolverines and 2 marten were entrapped in the tank, but remains included just one intact wolverine and scattered bone fragments; it was hypothesized that the intact individual, a female, had died of starvation after consuming the remains of all the other animals; a method of distinguishing sex from skull and dental measurements is described--the best results were given by greatest length of skull and antero-postero diameter of the maxillary canine.

Folk, G.E., Jr., M.A. Folk, and D. Craighead. 1977. A comparison of body temperatures of least weasels and wolverines. Comp. Biochem. Physiol. 58A:229-234.

044 A) 1; B) Alaska; C) Studies of captive animals.
Life History - nutrition, activity.
Other Topics - physiology.
Comments - Wolverines had higher resting body temperatures than the least weasels studied--comparisons with data for other mustelids suggest there is no correlation between body size and temperature in this group; temperature changes and other evidence indicated that the wolverines' daily activity patterns varied little between seasons, despite the great seasonal differences in day-length in the arctic, and that they were a "day-active' species (becoming very active in the morning, with bouts of sleep during the night).

Francis, G. 1960. Observations of some carnivores by wardens in the mountain national parks of Canada. Can. Field-Nat. 74:158-160.

045 A)1; B) Alberta, British Columbia; C) Compilation of sight records.
Life History - behavior.
Comments - 7 sightings are described for the years 1951-57, mostly in Banff and Jasper National Parks; two observations involved animals "playing" (groups of 3 and 2 in July 1951 and August 1954, respectively), two of pairs of animals traveling together (July 1954 and April 1957), and one of a pair of animals "either fighting or mating" (March 1957); one wolverine was observed to use the same large rock as a lookout overlooking an alpine meadow on several occasions over a four year period, and once left it briefly to chase a young bighorn ram that came by; a wolverine seen on the highway in Kootenay National Park was clocked at 15 mph.

Fry, W. 1923. The wolverine. Calif. Fish Game 9:129-134.

046 A) 1; B) California; C) Incidental field observations and reports.
Life History - food, behavior.
Population Dynamics - poptrend.
Comments - The wolverine is described as in danger of extinction in the state; it is said to occur in the high Sierra, at elevations of 6500- 13,000' (1975-3950 m), not descending to local lowlands even in winter; foods reported are carrion, yellow-bellied marmots, and smaller rodents such as "gophers" (ground squirrels?), rats, and mice--digging for rodents has been observed; a taste for porcupines, which results in death from quills in internal organs, is described as one of the factors hastening the species' demise, but no documentation is provided; instances of black bears, coyotes, and cougars giving up kills or carrion to wolverines is described in support of the author's label for the species as "king beast of the Sierras"; despite occasional damage to cabins and other property, a case is made for preserving the species.

Gardner, C.L. 1985. The ecology of wolverines in southcentral Alaska. Unpubl. M.S. Thesis, Univ. Alaska, Fairbanks. 82pp.

047 A) 3; B) Alaska; C) Field (telemetry) studies and analysis of a small sample of trapped specimens, 1979-82.
Description - features.
Habitat Characteristics - cover.
Life History - food, hmrange, movements, dispersal, socbehav, behavior.
Population Dynamics - mortality.
Species Management - age/tech, harvest.
Comments - Of 12 wolverines instrumented, 10 were males and most field study results apply primarily to that sex; animals were captured by darting from a helicopter, as trapping proved unsuccessful; **HOME RANGE AND TERRITORIALITY** - mean winter and summer home ranges for adult males were 353 km^2 and 385 km^2 respectively; the one male tracked for an entire year had winter and summer ranges of 515 km^2 and 451 km^2, respectively, and a total annual range of 637 km^2; there was little range overlap between adjacent animals, except between an adult and a juvenile, the latter eventually dispersing from the area; the summer range of a lactating female with 2 kits was 92 km^2; the Susitna River acted as a home range boundary for 6 of 7 males, but was not a barrier to their movement; **MOVEMENTS** - distinct seasonal shifts in elevation occurred, with animals moving up in spring (apparently mostly to hunt emerging ground squirrels) and down in late fall/winter to ungulate winter ranges; animals moved about regularly, but occasionally concentrated activity in one area for a period; the two factors leading to intensive local use were presence of a large carcass (used up to 27 days in one case) and breeding (pairs remaining together in a localized area 2-3 days); one carcass was used concurrently by a juvenile and adult male, with both there together in at least one occasion; **DISPERSAL** - two documented dispersals involved a 2-year old male that moved a minimum of 378 km, where it was trapped in the Yukon, and a juvenile male that moved 30 km before it was trapped; **HABITAT** - spruce communities and ecotonal areas (mostly rock outcrops) were

used significantly more than in expected in relation to availability--winter ground tracking showed that even though animals might be located in all habitats, they were not all of equal significance--they appeared to be coursing and hunting primarily in the spruce types and making straight- line movements (traveling) through tall shrub and deciduous forest communities; tundra communities were avoided in winter; **FOOD HABITS** - chief winter food items (colon analyses, N=35) by frequency and percent dry weight were moose (24.7, 41.1), caribou (20.0, 20.4), microtine (20.0, 6.7), and bird (11.4, 1.7); moose was the most common ungulate present, especially in winter, and most use appeared to be at wolf kills; among small mammals, red squirrel (8.6, 1.7), snowshoe hare (5.7, 0.8), porcupine (2.9, 1.7), and "beaver/muskrat" (2.9, 10.6) were also commonly used, and soil was a regular and large component (20.0, 15.4); caching and use of caches was not commonly recorded--wolverines and foxes often followed each other's tracks, probably looking for cached prey; summer food was believed to be chiefly ground squirrels, birds, and microtines; **FEATURES** - the average live weight for 10 males of all ages was 15.8 kg (range 14.1-17.7), and for 2 females was 10.0 (9.5- 10.0); **MORTALITY** - a male that died of undetermined "natural causes" was mostly eaten and the remains cached by another wolverine, apparently in late winter (found in mid-April); the most important mortality factor appeared to be harvest by humans, which apparently focussed primarily on juveniles; **HARVEST** - the recorded local harvest during 3 seasons was 103 males:73 females (1.4:1), a significant difference; most of the harvest was in February and March--males, especially the two immature classes, dominated in December, with females increasing in the harvest later on; **AGE DETERMINATION** involved use of dental cementum, with the canine believed to give better results than other teeth; **AGE COMPOSITION** of the local sample included 22 kits (43%), 15 subadults (29%), and 14 adults (28%); **MANAGEMENT CONSIDERATIONS** - analysis of the harvested sample plus the fact that 6 of 10 of the captured animals were adults was taken to indicate that the population was not being heavily harvested; it is noted that census of wolverines is not presently feasible and will not likely be in the near future, and that analysis of harvest samples can detect population changes (primarily composition) only after the fact.

Gardner, C.L., W.B. Ballard, and R. H. Jessup. 1986. Long distance movement by an adult wolverine. J. Mammal. 67:603.

048 A) 2; B) Alaska, Yukon Territory; C) Incidental field observation.
Life History - dispersal.
Comments - A radio-collared adult male wolverine (2 years old, 18.0 kg), after spending a minimum of 19 days within the home range of an older (7 year old) resident male in southcentral Alaska, left the area and was trapped about 20 months later in the Yukon, 378 km to the east.

Gavin, A. 1945. Notes of mammals observed in the Perry River district, Queen Maud Sea. J. Mammal. 26:226-230.

049 A) 0; B) Northwest Territories; C) Incidental observations and anecdotes.
Description - distribution.

Life History - behavior.
Comments - Wolverines are regarded as common in the area, and are said to "...follow the traplines in winter."

Gill, D. 1978. Large mammals of the Macmillan Pass area, Northwest Territories and Yukon. Rep., AMAX Northwest Mining Co. Ltd., Vancouver, B.C. 58pp.

050 A) 1; B) Northwest Territories; C) Incidental field observation.
Life History - food, behavior.
Species Management - economics, interactions.
Comments - A wolverine killed a young (ll months old) female Dall's sheep on 12 April 1978; the sheep was in poor physical condition, and tracking showed that the wolverine's advantage was further enhanced by the fact that it was sinking only 10-15 cm into the snow while the sheep was sinking 35-40 cm; tracking also showed that the wolverine had approached the band of sheep from above, cutting them off from escape terrain--it was noted that the wolverine's strategy suggested "learned predatory behaviour" and it was speculated that wolverine predation might be a significant mortality factor for sheep in the area; the wolverine's first and only meal from the sheep was the animal's head and neck, to the base of the cervical vertebrae; it then dug a nearby snow cave and slept there, but was apparently subsequently alarmed by the observers' helicopter and fled downslope to wooded cover; also on 12 April, another wolverine was killed and partly eaten ("all of the body posterior of the shoulders") by wolves; tracking indicated that it had visited and scavenged moose kill remains left by the wolves.

Goldman, E.A. 1935. New American mustelids of the genera *Martes*, *Gulo*, and *Lutra*. Proc. Biol. Soc. Washington 48:175-186.

051 A) 1; B) British Columbia; C) Examination of two museum specimens.
Description - features, taxonomy.
Comments - Description of the Vancouver Island form as a subspecies, judged smaller than mainland forms based on skull measurements.

Gonyea, W., and R. Ashworth. 1975. The form and function of retractile claws in Felidae and other representative carnivores. J. Morphol. 145:229-238.

052 A) 0; B) General; C) Detailed anatomical dissections of the feet of several carnivores.
Life History - behavior.
Other Topics - morphology.
Comments - Unlike felids and some viverrids, wolverines mainly use the jaws rather than claws for capturing and holding prey, and their anatomy differs accordingly; the wolverine is characterized as primarily a terrestrial hunter but is also "quite scansorial" (tree climbing), and "...is probably one of the most generalized of carnivorans in terms of its anatomy and behavior."

Grinnell, G.B. 1920. As to the wolverine. J. Mammal. 1:182-184.

053 A) 1; B) General; C) Literature review and account of anecdotes.
Life History - behavior.
Species Management - interactions.
Comments - Accounts are given of wolverines killing moose and caribou, having somehow got onto the backs of the animals and biting from there; reports confirm that wolverines can climb--in one case the fact that a wolverine climbed a tree when chased by dogs suggests that use of trees as refuge from wolves may be a regular part of the species behavioral repertoire.

Grinnell, G.B. 1921. The tree-climbing wolverine. J. Mammal. 2:36-37.

054 A) 0; B) Alaska; C) Compilation of anecdotes.
Life History - behavior.
Comments - Anecdotes from Alaska, involving the plundering of tree caches by wolverines, are given as further evidence of the climbing ability of the species.

Grinnell, G.B. 1926. Some habits of the wolverine. J. Mammal. 7:30-34.

055 A) 0; B) General; C) Compilation of anecdotes.
Life History - behavior.
Species Management - interactions.
Comments - More wolverine stories, including account of an attack on a cow elk that resulted in a wound, on the animal's back, severing the spinal cord (similar to an injury described for an attacked moose in Grinnell 1920); in two other instances, evidence is presented that wolverines mortally injured a cougar and a bear (species not given); an arctic explorer is quoted as writing that "Hardly any kind of a cache can be made strong enough to keep out a wolverine if he has plenty of time to work undisturbed, for the animal is strong enough to roll away heavy stones and logs, gnaw through timbers, climb to elevated caches, and excavate buried goods. We lost a shotgun which was hung on a tree, carried away by a wolverine."

Guiguet, C.J. 1951. An account of wolverine attacking mountain goat. Can. Field-Nat. 65:187.

056 A) 1; B) British Columbia; C) Incidental field observation.
Life History - food, behavior.
Species Management - interactions.
Comments - Twice in the same day (1 August 1951), a wolverine was observed in pursuit of mountain goats in northcentral B.C.; on the second occasion it caught a nanny by the hind leg, but she escaped in the ensuing struggle, threw the wolverine with her horns, and successfully stood it off thereafter.

Haglund, B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. Viltrevy 4:81-299.

057 A) 2; B) Sweden; C) Snow-tracking, winters of 1960-64.
Habitat Characteristics - vegetation.
Life History - food, activity, movements, behavior, socbehav, denning.
Species Management - economics, interactions.
Comments - A total of 957 km of wolverine trails was followed, mostly in late winter (March and April); during winter "...most of the wolverines live in the low mountains or in the coniferous forest bordering on the high mountains"; daily activity is irregular, showing no distinct pattern--the species is described as the most likely of the four large European predators to be seen in "bright daylight"; daily movements were difficult to determine because of the irregular activity pattern, but "...a normal distance seems to be at least 30 km"; the primary winter food was reindeer, occurring in 32 of 38 scats (84%)--other scat occurrences were rodents in 10 (26%), and a variety of plants fragments and bone material; the small mammals in the scats included 22 individuals--18 lemmings, 2 unident., 1 vole, and 1 shrew; of 50 reindeer kills visited by wolverines, it was believed that 15 had actually been killed by the wolverines and at least another 20 by lynx-- wolves are rare in the area and lynx are said to have taken over that species role of providing meat for wolverines; wolverines are unskillful hunters, chasing prey when the opportunity presents itself but doing so clumsily--none of 7 chases of hares or tetraonids were successful, and pursuits of reindeer were successful only in late winter when snow conditions favored the wolverine and (possibly) when the reindeer were in poorest physiological condition; attacks were usually on the backs of prey animals, with bites directed to the neck and/or spine; the wolverine was considered less likely than other predators to take prey in prime condition; wolverines showed a particular interest in lynx tracks in early winter (before March), following them an average of 5 km when they were encountered, but showed little interest in them in March and April when numerous carcasses were available--the distance between carcasses was 23.9 km before March, 8.7 km in March, 12.9 km in April, and 7.1 km in May; food storage (caching) is a conspicuous part of the wolverine's behavior, and is accomplished most often by digging it down into the snow; occasional removal of a prey animal's head was noted; territorial marking by biting into small trees and by deposits of urine and feces were noted; wolverines were mostly solitary in winter, but there were several records (particularly in late March) in which two adults, believed male and female, traveled together for a time; natal dens were most commonly snow caves amid rock formations in the mountains, but "...might be found below the limit of coniferous forests...usually among the rocks...below a mountain slide"; there was some indication that natal denning areas were selected in areas where stored carcasses had accumulated.

Haglund, B. 1974. Moose relations with predators in Sweden, with special reference to bear and wolverine. Naturaliste Can. 101:457-466.

058 A) 0; B) Sweden; C) Review of literature and anecdotes.
Life History - food, behavior.

Species Management - economics.
Comments - Cases of wolverines killing moose, usually after the moose had already been injured or was incapacitated in deep snow, are cited, but are considered rare and unusual events with no population consequences; also cited is a Soviet report of three different instances in which pregnant cow moose aborted when chased by wolverines, and the wolverines subsequently ate the aborted fetuses.

Hall, E.R. 1926. Abdominal skin gland of *Martes*. J. Mammal. 7:227-228.

059 A) 0; B) General; C) Laboratory examination of specimens.
Life History - socbehav.
Other Topics - morphology.
Comments - Conspicuous abdominal skin glands, possibly used in chemical signaling, were found in martens and wolverines, but not in fishers, weasels, mink, otters, civets, or skunks.

Hansson, I. 1970. Cranial helminth parasites in species of Mustelidae. II. Regional frequencies of damage in preserved crania from Denmark, Finland, Sweden, Greenland and the northeast of Canada compared with the helminth invasion in fresh mustelid skulls from Sweden. Ark. Zool. (Stockholm) 22:571-594.

060 A) 1; B) Scandinavia; C) Laboratory examination of skulls.
Life History - health.
Comments - Among 102 wolverine skulls from Sweden (63) and Finland (39), only 1 (1%) showed evidence of sinus worm damage--that was an adult female from Finland.

Hantzsch, B. 1932. Contributions to the knowledge of extreme northeastern Labrador. Can. Field-Nat. 46:7-12, 34-36.

061 A) 0; B) Labrador; C) Literature review and anecdotal information.
Description - distribution.
Comments - Wolverines are considered rare in the northeast, but are believed more common to the south.

Hardy, T.M.P. 1948. Wolverine fur frosting. J. Wildl. Manage. 12:331-332.

062 A) 0; B) General; C) Experiments with museum or other specimen material.
Life History - pelage
Comments - To evaluate materials for use in outer garments to be used by explorers and workers in the arctic, various fur samples were sprayed with water from an atomizer and then placed in a freezer; three of the sample materials (alpaca pile, wolf, and coyote) always became caked and matted with ice, but wolverine guard hairs always remained ice free (despite some ice crystal formation in the underfur); microscopic examination indicated that the ice resistance of wolverine fur is due to difference in length between guard hairs and underfur, the straightness of the guard hairs, the extreme density of the underfur, and the higher angle of insertion of all hair fibers as compared to those in the other species.

Harper, F. 1932. Mammals of the Athabaska and Great Slave Lakes region. J. Mammal. 13:19-36.

063 A) 0; B) Northwest Territories; C) Anecdotal information.
Description - distribution.
Life History - behavior.
Comments - Wolverines are listed as present, with anecdotes focussing on depredations to human property.

Hash, H.S. 1987. Wolverine. Pages 575-585 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch (eds). Wild furbearer management and conservation in North America. Ontario Trappers Assoc., North Bay.

064 A) 2; B) General; C) Literature review.
Description - features, distribution, taxonomy.
Habitat Characteristics - vegetation, cover.
Life History - lifehist, denning.
Population Dynamics - mortality, natality, poptrend.
Species Management - census, economics, harv/strategy, transplants.
Other Topics - history.
Comments - This is an excellent review of wolverine biology and management, including results from all significant studies through 1985, but because it largely draws on literature described in detail in the present annotated bibliography, it will not be extensively quoted--only new information and/or unique interpretations follow; the point is made that the northward diminution of the historical range on this continent commenced in the mid-1800's, coincidental with increased European exploration and settlement and expansion of the fur trade, and decline of the northern bison; the boreal forest, most of which is remote and little affected by development, is presently "...the largest geographic area of occupied wolverine habitat"; two pregnant females recently killed in early March in Montana contained fully developed fetuses, and "several" litters 2-3 weeks old have reportedly been observed in that state in March; natal dens in Montana are most commonly associated with snow-covered tree roots, logjams, or rocks and boulders; wild wolverines harvested in Montana rarely exceed 8 years of age, and the average is 4- 6; a 1937 reference from California is cited as reporting that dead wolverines had been found with their stomachs and digestive tracts impacted with masses of porcupine quills; population assessment may be best accomplished by use of indirect indices, with use of bait stations to attract animals; reintroduction to areas of former habitat is recommended to assist in population recovery--releases in the ratio of 2-4 females per male is recommended; "Carefully regulated harvest programs, the implementation of refined monitoring techniques, appropriate reintroduction programs, and the preservation of adequate suitable habitat should ensure the survival of the wolverine for future generations."

Hash, H.S., and M.G. Hornocker. 1980. Immobilizing wolverines (*Gulo gulo*) with ketamine hydrochloride. J. Wildl. Manage. 44:713-715.

065 A) 1; B) Montana; C) Field testing of the drug.
Description - features.
Species Management - gen/tech.
Comments - Ketamine administered in dosages of about 20 mg/kg body weight produced satisfactory results with no mortalities in 24 immobilizations; onset of immobilization occurred in an average of about 4 minutes for both sexes; males were immobilized for shorter periods (about 30 vs. 45 minutes), and recovered more quickly than females; gentle handling and holding in an enclosure until complete recovery (several hours) is recommended.

Haugen, A.O. 1961. Wolverine in Iowa. J. Mammal. 42:546-547.

066 A) 1; B) Iowa; C) Report of an animal shot, May 1960.
Description - features, distribution.
Life History - food, health.
Comments - An adult female wolverine, weighing 22 lbs (10.0 kg), was pursued and shot in a cornfield; the animal had badly worn teeth and 2 or more toes missing from 3 of its feet (those wounds well healed), suggesting several past encounters with traps; the animal showed no sign of recent pregnancy; stomach contents included carrion (probably cow), and shells from ground-nesting birds, including pheasant; parasites found included 23 ascarids (*Physaloptera* spp.) among the viscera and *Trichinella* larvae in a muscle tissue sample; the author was doubtful that the animal had arrived in Iowa under its own power, but had no certain information to the contrary.

Hoak, J.H., J.L. Weaver, and T.W. Clark. 1982. Wolverines in western Wyoming. Northwest Sci. 56:159-161.

067 A) 1; B) Wyoming; C) Compilation of sightings from interviews and voluntary reports.
Description - distribution.
Population Dynamics - poptrend.
Comments - A total of 50 records, 5 involving more than one animal (including family groups), were assembled for the area of western Wyoming outside Yellowstone National Park in the 1960's and 1970's; the increased number of sightings in comparison to 4-5 decades previous is thought to be the result of "...increased human use of remote areas, an extension of wolverine range, or both"; the ban on use of poisons for predator control on federal lands is considered beneficial to carrion feeders such as the wolverine.

Holbrow, W.C. 1976. The biology, mythology, distribution and management of the wolverine (*Gulo gulo* L.) in western Canada. M.N.R.M. Practicum, Univ. Manitoba, Winnipeg. 214pp.

068 A) 2; B) Canada; C) Review of literature and anecdotes.
Description - distribution.
Life History - lifehist.
Population Dynamics - poptrend.
Species Management - economics, harv/strategy.
Other Topics - history.
Comments - In its compilation of wolverine lore, legend, and anecdotes, this document is second to none, but the review was undertaken prior to any significant field studies on the species on this continent--only new or unique information, not described elsewhere in the present bibliography is given below; an unpublished winter tracking study in Mt Assiniboine Prov. Park, B.C. (Cockerton and Herrero 1973) reported movements of 25 km...in several hours, 25-30 km in another case, and 120 km in a third...with no obvious signs of rests or pauses"; a wolverine shot in a mining camp in the Northwest Territories was apparently dragged away by another wolverine within two hours, and portions of it were eaten in the approximately 5 km the tracks were followed, until the remains were left behind; trapper activity and wolverine population status information was obtained by interviews and questionnaires for Manitoba, Saskatchewan, Alberta, British Columbia, Yukon and Northwest Territories--only significant information and interpretations for B.C. are given below; of 156 B.C. respondents to a questionnaire for trappers, 104 (67%) had set traps specifically for wolverine--for the entire western Canada study area, the figure was 182 of 344 (53%); most B.C. trappers (56 of 72 = 78%) used killer traps (mostly conibears, deadfalls, or snares) when setting for wolverine; changes in wolverine abundance in B.C., as indicated by harvest returns and sightings records, "...are much less pronounced than (for) any other province or territory in the study area"; one trapper from the Stewart area of B.C. noted that after January he takes no female wolverine (implying that they had disappeared by then...); fur production records do not support the contention that wolverines have a 10-year cycle, and most trappers did not believe that to be true--it was noted, however, that the animals might appear on a trapline one year and not the next; the species is not overly important economically--one trapper noted that "If a guy had to depend on...all the wolverine he caught, he'd be one hungry S.O.B..."; wolverines have often been trapped because of their reputation for damage or as predators rather than for fur value; although generally ranked as the most damaging species on a trapline (slightly ahead of wolf), total annual damage estimates by trappers were about $250 (with only a portion of that due to wolverines); further, only 128 of 394 trappers (32%) had ever experienced damage by wolverines (63 of 178 = 35% in B.C.), and only 31 of 153 (20%) felt that wolverines were a negative influence on the local fur industry (13 of 54 = 24% in B.C.); termination of the open season for hunting throughout B.C., and closed seasons for trapping in several areas of the province are recommended.

Holland, G.P. 1941. Further records of Siphonaptera for British Columbia. Proc. Entomol. Soc. B.C. 37:10-14.

069 A) 1; B) British Columbia; C) Incidental record from 1 specimen.
Life History - health.
Comments - This paper includes a record of the flea *Diamanus montanus* (Baker) on a wolverine from the Eagle River.

Holland, G.P. 1949. A revised check list of the fleas of British Columbia. Proc. Entomol. Soc. B.C. 45:7-14.

070 A) 1; B) British Columbia; C) Review of data.
Life History - health.
Comments - This is a listing of flea occurrence without details on numbers of host animals examined or extent and significance of infestations; among 93 species of fleas listed, the wolverine is named as a "recorded host" for only 2--*Chaetopsylla setosa* (Rothschild) ("true hosts: various large carnivores") and *Thrassis spenceri* Wagner ("true host: Alpine marmot, *Marmota caligata* group"); the record of *Diamanus montanus* in Holland (1941) is corrected to *Thrassis*, as above.

Hornocker, M.G., and H.S. Hash. 1981. Ecology of the wolverine in northwestern Montana. Can. J. Zool. 59:1286-1301.

071 A) 3; B) Montana; C) Field studies, including live-trapping and marking, snow-tracking, and telemetry, 1972-1977.
Habitat Characteristics - study/area, cover.
Life History - food, hmrange, movements, dispersal, socbehav, behavior.
Population Dynamics - natality, mortality, poptrend, popcomp.
Species Management - gen/tech, harv/strategy, refuges.
Habitat Management - forestry, hab/strategy.
Comments - This was the first intensive field study of wolverines in North America, and detailed coverage here is warranted; it is noted that within the contiguous 48 states, only Montana had "...adequate numbers to constitute viable populations"; a total of 24 different individuals were captured and marked during the study, including 11 males (9 adults and 2 subadults) and 13 females (8 and 5); **FOOD HABITS** - large wild and domestic ungulates, all believed taken as carrion, predominated in 56 winter scats collected during the study period, with deer or elk in 15 (27%), domestic cow in 15 (27%), and horse in 10 (18%); other food items identified, and frequencies, were snowshoe hare (9 occurrences, 17%), marmot (6, 11%), beaver (3, 6%), small rodents (3, 6%), birds (3, 6%), and porcupine (2, 4%); food caching was not a conspicuous feature of wolverine behavior on the study area, and it is speculated that it may be important in population dynamics "...only in areas where other scavenging species are scarce and where permafrost exists; incidence of marmot in winter scats was believed to represent predation on hibernating animals; Columbian ground squirrels were abundant in some areas frequented by wolverines, especially in spring when

they are believed particularly vulnerable to predation, and it is believed that "...wolverines preyed heavily on the squirrels"; **MOVEMENTS** - mean movements between relocations of radio-collared animals were greatest during spring and summer, and greater for males than for females-- maximum 3-day movements were 64 km for males and 38 km for females; **HOME RANGE** - mean home ranges for males and females, respectively, were 422 and 388 km^2--lactating females showed reduced spring and summer ranges (about 100 km^2); individuals of both sexes showed fidelity to particular areas, but some made long movements away from those areas for periods of up to 30 days; **HABITAT** - both sexes used higher elevation habitats in spring and summer than in winter--mean elevation of radio- locations during the 4 seasons were winter -1371 m, spring - 1676 m, summer - 1920 m, and fall - 1889 m; all aspects were used, but "...easterly and southerly areas received the majority of consistent use"; 70% of all relocations were in medium density or scattered mature timber, while most of the rest were in ecotonal areas--dense young timber, burns, and wet meadows were rarely used; "wet timber, dry timber, and alpine areas composed 23, 31, and 16%, respectively, of all relocation sites; wolverines selected *Abies* forest types, occurring there in 56% of locations despite the fact that it constituted only 27-42% of available cover--that selection was particularly pronounced in summer; no wolverines were relocated in clear cuts of any size, although tracks crossing clearcuts were observed 15 times--tracking showed that "...wolverines meandered through timber types, hunting and investigating, but made straight line movements across large openings" (usually at a lope or gallop); bed sites were often in snow on open outcrops "...all in timber types which afforded cover"; geographic barriers such as mountains and large rivers do not confine wolverine populations as they do other species, therefore the populations "...must be treated as regional rather than local"; **NUMBERS** - a minimum of 20 wolverines were estimated for the 1300 km^2 study area, for a density of 1 animal/65 km^2--that density is higher than reported elsewhere, possibly because of the high density and diversity of available ungulates in the area; **MORTALITY** - 18 mortalities were recorded during the study, including 15 animals taken by trappers (9M, 5F, 1U--5 of the 15 marked) and 3 collared animals dying of "natural causes"; the natural deaths included an apparently "old" female that was diagnosed as dying from a uterine infection, and two animals (an old male and a subadult female) that apparently died of starvation--both relied heavily on trap baits before death, and were captured repeatedly; one female wolverine sustained injuries believed to have been caused by a mountain lion, and many of the captured adults were missing toes and/or had broken teeth, probably indicating encounters with traps; **REPRODUCTION** - of 15 female reproductive tracts in preimplantation condition, a mean of 2.93 corpora lutea were found and among 6 tracts with implanted embryos or fetuses the mean number was 2.17, suggesting that "...productivity in our area may be lower than in Alaska"; capture-recapture data indicated that females did not produce young every year and it was believed that "...no more than half the females present...were reproductively active in each of the 5 years..."; **DISPERSAL** - kills from outside the study area indicated that dispersal of young from the area occurred; **TERRITORIALITY** - range overlaps between and among the sexes were common and territorial defense was not apparent--it is speculated that the observed pattern reflects either the animal's scavenging life style (in which flexibility of movement is required and maintenance of a large exclusive area would

be difficult), or the fact that turn-over in the population was too rapid to enable individuals time to develop their full territorial system; **MANAGEMENT CONSIDERATIONS** - wolverines used "wilderness" and "non-wilderness" areas equally, but were in the nonwilderness (logging and recreation area) primarily in winter, when human activity there was least, and were high in adjacent, rugged mountains during much of the snow-free season; the wolverine has long been regarded as a pest over most of its range, and its relatively low fur value has resulted in its not being a priority for conservation, but in 1975 Montana removed the "predator" classification and introduced more stringent harvest regulations including a distinct trapping season and a season limit of 1 animal per trapper--the annual take has "declined markedly" as a result; "wolverines come readily to bait and are vulnerable to skilled trappers" and it is therefore recommended that "...bait trapping for all species...be curtailed" where enhancement of wolverine populations is the goal; it is also recommended that seasons be closed during the late winter and early spring when the young are born; "Wolverine populations in northwestern Montana survived the years of unlimited hunting and trapping solely because of the vast expanses of official wilderness and remote, essentially wilderness habitat..." (which) "...functioned as both refuge and reservoir for wolverine populations."

Hornocker, M.G., J.P. Messick, and W.E. Melquist. 1983. Spatial strategies in three species of Mustelidae. Acta Zool. Fennica 174:185-188.

072 A) 2; B) Montana; C) Literature review.
Life History - dispersal, socbehav.
Comments - Wolverines marked profusely, but displayed little territorial defense by aggression; individuals showed fidelity to particular areas, but occasionally left them, apparently mostly in response to food availability considerations; young animals dispersed long distances, up to 150 km recorded, and males made seasonal movements during the breeding season; "The scavenging lifestyle of this species dictates long seasonal movements, a relatively large home area, and a solitary existence"; strict maintenance of territories would be difficult, given their large size, and would not seem advantageous to a species largely dependent on carrion--"a system which provides for flexibility of movement to areas of carrion abundance would appear to be more successful"; it is concluded that the three species (wolverine, otter, badger) have a flexible behavioral system that "...may be regarded as a positive adaptation to different and changing environments and is of value to the species' survival"; "From our data, we would expect to encounter different spatial strategies in any of these three Mustelidae anywhere, with this strategy wholly dependent upon external and internal influences acting on any particular population."

Houston, D.B. 1978a. Elk as winter spring food for carnivores in northern Yellowstone National Park, Wyoming, U.S.A. J. Appl. Ecol. 15:653-662.

073 A) 1; B) Wyoming; C) Monitoring of elk mortality and use of carcasses.
Description - distribution.
Life History - food.

Comments - Winter-killed elk provide an important source of protein for a number of wildlife species in the park--wolverine listed, but population status considered "uncertain"; differences in food availability in different years (related to winter severity) are documented.

Houston, D.B. 1978b. Cougar and wolverine in Yellowstone National Park. Res. Note No. 5, Yellowstone National Park.

074 A) 1; B) Wyoming; C) Compilation of records of sightings.
Description - distribution.
Life History - food.
Comments - Not seen: cited in Hoak *et al.* (1982)--27 records of wolverine occurrence in the park documented for the period 1970-78; the winter distribution there generally coincided with ungulate winter ranges where carrion was available.

Iverson, J.A. 1972a. Basal energy metabolism of mustelids. J. Comp. Physiol. 81:341-344.

075 A) 0; B) General; C) Studies of captive animals.
Other Topics - physiology.
Comments - Measurement of basal metabolism in 7 species of mustelids, including wolverine, showed that those species weighing 1 kg or more had about 20% higher levels than predicted by the general curve for mammals of comparable size, and much higher (to 100%) for the species below 1 kg (weasel and stoat).

Iverson, J.A. 1972b. Basal metabolic rate of wolverines during growth. Norwegian J. Zool. 20:317-322.

076 A) 0; B) Norway; C) Studies of captive animals.
Life History - nutrition.
Other Topics - physiology.
Comments - Features of changing metabolism in young growing wolverines are described, but with no population or management implications.

Jackson, C.F. 1922. Notes on New Hampshire mammals. J. Mammal. 3:13-15.

077 A) 0; B) New Hampshire; C) Review of literature and anecdotes.
Description - distribution.
Comments - An observation of two young wolverines in 1918, Connnecticut Lakes area, "...would lead one to believe that the species was breeding to a certain extent within this wild region."

Jackson, H.T. 1922. Wolverine in Itasca County, Minnesota. J. Mammal. 3:53.

078 A) 0; B) Minnesota; C) Record of an animal killed, January 1899.
Description - distribution.
Other Topics - history.
Comments - A museum specimen record (adult male) is documented in response to a previous report, which suggested that there had been no known occurrences of the species in that area.

Jackson, H.T. 1954. Wolverine (*Gulo luscus*) specimens from Wisconsin. J. Mammal. 35:254.

079 A) 0; B) Wisconsin; C) Examination of skeletal remains.
Description - distribution.
Comments - Noting that there have been authentic sightings but no specimen records either for Wisconsin or for Michigan (the "Wolverine State"), the author refers to a femur of a young female, found in a Wisconsin cave in 1920 (but possibly deposited there as early as 1870); this is listed as the most southerly record for the state, and is about 40 km south of a location where a wolverine was reportedly shot in 1855.

Jackson, H.T. 1961. Mammals of Wisconsin. Univ. Wisconsin Press, Madison.

080 A) 0; B) Wisconsin; C) Literature review.
Description - distribution.
Life History - lifehist.
Comments - Cited as a "very useful" paper by Dagg and Campbell (1974a), but containing no "new" information, i.e., nothing that is not available in other references listed here.

Johnson, C.E. 1923. A recent report of the wolverine in Minnesota. J. Mammal. 4:54-55.

081 A) 0; B) Minnesota; C) Anecdotal records.
Description - distribution.
Population Dynamics - poptrend.
Comments - Record of a "green pelt" from an animal possibly taken in St. Louis County in 1918--the fur buyer noted that he had only bought 1 wolverine skin in 3 years in that area and adjacent Canada; the buyer believed that the species had been scarce for the previous 20-30 years, but not extirpated.

Johnson, C.E. 1930. Mammals of northwestern Minnesota. J. Mammal. 11:435-452.

082 A) 0; B) Minnesota; C) Review of literature and anecdotes.
Description - distribution.
Comments - Two second-hand reports of past wolverine kills are given (1890 and late 1880's or early 1890's), but the absence of subsequent records leads to the conclusion that "...the species has been extinct in this state for some time."

Johnson, R.E. 1977. An historical analysis of wolverine abundance and distribution in Washington, U.S.A. Murrelet 58:13-16.

083 A) 1; B) Washington; C) Literature review and compilation of sight and specimen records.
Description - distribution.
Population Dynamics - poptrend.
Other Topics - history.
Comments - Evidence is presented suggesting that wolverines were present in the Cascade Range between 1890 and 1919, may have been absent or were at least exceedingly rare there and elsewhere in the state from 1920 through 1959, but re-appeared, increased and expanded their range dramatically in the 1960's and early 1970's; "...individuals apparently began to move southward from Canada, perhaps indicating a reduction in trapping north of the border....this trend, combined with legal protection in Washington starting in 1955, has apparently led to the range expansion seen today."

Jones, F.L. 1950. Recent records of the wolverine (*Gulo luscus luteus*) in California. Calif. Fish Game 36:320-322.

084 A) 0; B) California; C) Literature review and compilation of anecdotes.
Description - distribution.
Population Dynamics - poptrend.
Comments - Records of 16 wolverine sightings, 1927-1947, are presented, although the general conclusion that the species is rare and/or declining in the area does not change; one record is of 6 wolverines seen together in Sequoia National Park in the early 1930's.

Jones, F.L. 1955. Records of southern wolverine, *Gulo luscus luteus*, in California. J. Mammal. 36:569.

085 A) 0; B) California; C) Compilation of sight and specimen records.
Description - distribution.
Comments - A total of eight new observations of animals and/or tracks and 1 record of an animal killed by a deer hunter are documented for the period 1938-1953.

Kauranen, P., J.K. Miettinen, and E. Pulliainen. 1971. Polonium-210 and lead-210 in some terrestrial animals in Finland. Ann. Zool. Fenn. 8:318-323.

086 A) 0; B) Finland; C) Laboratory analyses of tissue samples.
Life History - food, health.
Habitat Management - other/nat.
Comments - These radionuclides, from "natural fall-out", apparently are diluted slowly in the arctic ecosystem, and concentrations were found in various herbivores, especially reindeer and ptarmigan, and their predators (including wolverines); the highest levels were in samples from farthest north, in Lapland, but were not believed to be sufficient to have genetic or health consequences.

Kebbe, C.E. 1966. Wolverine killed in Oregon. Murrelet 47:65.

087 A) 1; B) Oregon; C) Report of an animal killed, September 1965.
Description - features, distribution.
Comments - The large male, weighing 28 lbs (12.7 kg), constituted the first specimen record since 1912; reference is made to "...several unverified reports....in the last five years" which indicate that a remnant population may still exist in remote areas of the Cascade Range.

Kelsall, J.P. 1981. Status report on the wolverine, *Gulo gulo*, in Canada in 1981. Comm. Status Endangered Wildl. Can., Ottawa. 47pp.

088 A) 2; B) Canada; C) Literature review and interview of government wildlife managers.
Description - taxonomy, distribution.
Life History - lifehist.
Population Dynamics - poptrend, popreg.
Species Management - harv/strategy, transplants, refuges.
Comments - This is an excellent review of then existing information; fur harvest and sightings data suggest declines in overall numbers in the past decade, and that result may be related to increased pelt prices; "the primary limiting factors are believed to be predation by humans, reduction of habitat by encroaching civilization, and availability of food, particularly carrion from large ungulates, in winter"; included among "predation by humans" is the incidental kill of wolverines by past wolf poisoning programs (1 wolverine per 8.9 wolves documented at bait stations in northern Canada); harvest regulations in the various Canadian jurisdictions are reviewed--most are liberal, and some significance is attached to the fact that open seasons are maintained during the whelping season; up to 50% of the wolverine pelts sold annually in Canada in recent decades have come from British Columbia; knowledge of the species is considered "insufficient to recommend sound management measures", and the major recommendations are for increased research and monitoring; it is concluded that "as a scavenger on the peripheries of the food web, requiring huge areas of wilderness as home range, the wolverine does not lend itself readily to direct management programs"; maintenance of important food resources, particularly the large caribou herds of the north and the diverse ungulate faunas of the western mountains and large national parks is considered fundamental to maintenance of wolverine populations in Canada.

Koehler, G.M., M.G. Hornocker, and H.S. Hash. 1980. Wolverine (*Gulo gulo*) marking behavior. Can. Field-Nat. 94:339-341.

089 A) 2; B) Montana; C) Field observations, snow-tracking.
Life History - socbehav.
Comments - Four types of scent marking were observed: 1) deposition of musk on a tree trunk or on the ground, 2) scratching the ground (with or without musk deposition, 3)

gnawing or biting a limb or root scented with musk, and 4) deposition of scat or musk on the ground without leaving visual signs; the first type, which usually involved climbing the tree, comprised 70% of 157 recorded marking sites; musk was seen and smelled on trunks an average height of 46 cm and as high as 74 cm from the base; one wolverine marked 20 different sites in 2.5 km of travel; marking sites tended to be on prominent trees in an area, but sometimes were on scats left by other species (e.g., coyotes), hummocks of snow, small trees, and rocks; some sites were known to have been marked by at least two different individuals; males were documented marking on 4 occasions, but no positive evidence of female marking was obtained; it is speculated that marking may be useful primarily for maintaining time rather than area spacing--i.e., indicating an area is occupied and facilitating avoidance by others; from the energy expended and attention given, it is concluded that marking behavior is an important form of communication among wolverines.

Kovach, S.D. 1981. Wolverine, *Gulo gulo*, records for the White Mountains, California. Calif. Fish Game 67:132-133.

090 A) 1; B) California; C) Literature review and report of an incidental field observation.
Description - distribution.
Comments - A total of three sight records over a 40 year period (1937, 1960, and 1977) are cited as indicating that the Sierra Nevada Range may not be the only mountains used by wolverines (past and present) in California; the most recent sighting, in early July, involved two animals of somewhat different sizes that went under a boulder (possible den site) on a talus slope.

Krott, P. 1953. Recovery of a wolverine that had escaped during transport. Zeitschr. Tierpsychol. 10:254-268.

091 A) 0; B) Europe; C) Observations of a captive animal.
Life History - behavior.
Comments - A "tame" wolverine that escaped from a truck evaded attempts to find it until its "master" separated from strangers in the search; the incident is given as another example of extraordinary learning powers of the species in relation to self preservation.

Krott, P. 1957. Das heutige vorkommen des vielfrasses (*Gulo gulo* L.) in Europe. Zeitschr. Saugetierk. 22:208-213.

092 A) 1; B) Europe; C) Literature review.
Description - distribution.
Habitat Characteristics - vegetation.
Species Management - interactions.
Comments - From English summary: "The strong connection of the wolverine with the biotope of the northern coniferous forest is caused by a biotic factor, the wolf..."; it is also noted that the range of the species in Europe has changed little during historical times because "...it habits and behavior makes it difficult to be captured by man."

Krott, P. 1959a. Der vielfrass (the wolverine). Monographien der wildsaugetiere. Band XIII. Gustar Fischer Verlag, Jena. 159pp.

093 (All in German; not summarized--see account for Ewer 1973)

Krott, P. 1959b. How to hunt wolverine. The Beaver 290 (autumn):48-51.

094 A) 1; B) Finland; C) Popular account of findings (Lit. Review).
Habitat Characteristics - cover.
Life History - behavior, denning.
Comments - the general procedure for tracking a wolverine to a natal den is described; den sites in mountain areas are often a cave or cleft in the rock, but in the forest may be a hollow in a snowdrift under a fallen tree or under thick blowdown; natal dens are usually in or near "marshland", and an open stream or spring is usually nearby; it is emphasized that the trail to a wolverine's den may be very long and through very rough terrain, and that the species is competent at deception.

Krott, P. 1960. Ways of the wolverine. Nat. Hist. 69:16-29.

095 A) 3; B) Sweden; C) Observations of both wild and free-ranging captive animals.
Habitat Characteristics - cover, climate.
Life History - food, activity, socbehav, behavior.
Population Dynamics - natality.
Species Management - interactions.
Comments - This is a unique perspective on behavioral attributes of the species, which is considered uniform throughout its circumpolar range; its primary habitat is listed as "swamp areas of the northern coniferous forest region", to which it has become "ecologically bound" through its relationship with the wolf--the wolf is believed to largely exclude the wolverine from firmer ground and more open areas (in summer) both by competition and predation; the species is territorial, with boundaries marked by glandular secretions, urine, and feces and respected by other individuals; foods, in addition to carrion include eggs of ground nesting birds, wasp larvae, and berries--the animal functions as a predator of larger mammals only in winter, when snow conditions provide an advantage; despite its reputation for voracity, it shows no particular interest in new food opportunities after it has already eaten; a conspicuous feature of wolverine feeding behavior is caching of remains, usually by burying in snow or underground, but sometimes by wedging among branches of a tree; the species is not strictly diurnal or nocturnal--rather, it tends to be active for 3-4 hours and then at rest for a similar period, that pattern occurring in a more or less continuous cycle--bad weather (heavy snowstorms or rainfall) may result in longer periods of rest (up to days) and certain favorable weather conditions and/or extreme hunger may prolong activity for long periods; the age of sexual maturity is given as 4 years, and females are believed to breed only every 2-3 years, keeping the young with them until the age of 2 years; the havoc created in trappers' cabins and caches is relegated to "play", for which the

species is ascribed a tendency approaching that of otters; other behavioral features of relevance to management include a very cautious and suspicious nature, and the ability to learn and change behavior as required--reference is made to the species "...extraordinary ability to evade dangers...(which is)...far superior to any other northern mammal, including the wolf" and to a "considerable immunity to poison" with the animals able to withstand strong doses of strychnine; it is concluded that "...we detest most what we cannot subdue. All the superstition of the north regarding the wolverine can be attributed to ...(its) apparent invincibility."

Krott, P., and C. Gardner. 1985. Wolverine breeding behavior in Alaska. Saugietierk. Mitt. 32:87.

096 A) 1; B) Alaska; C) Incidental field observations.
Life History - behavior.
Population Dynamics - natality.
Comments - not seen; cited in Banci (1987).

Kurten, B. 1970. The neogene wolverine *Plesiogulo* and the origin of *Gulo*. Acta Zool. Fenn. 131:3-22.

097 A) 0; B) Holarctic; C) Examination of museum specimens and literature review.
Description - taxonomy.
Other Topics - paleontology, evolution.
Comments - Allometric comparisons indicate that the extinct *Plesiogulo* of Asia shows skeletal features intermediate between martens and wolverines, and that "a descent of *Gulo* from *Plesiogulo*, and of the latter from marten-like ancestors, is indicated".

Kurten, B., and R.L. Rausch. 1959. Biometric comparisons between North American and European mammals. I. A comparison between Alaskan and Fennoscandian wolverine (*Gulo gulo* Linnaeus). Acta Arctica 11:1-20.

098 A) 1; B) Holarctic; C) Examination of museum specimens (skulls).
Description - taxonomy.
Other Topics - paleontology, zoogeography, morphology.
Comments - Statistical comparisons of skull and dentition dimensions show that the existing Palearctic wolverine has a somewhat larger skull and smaller teeth than its Nearctic counterpart, but the two forms are sufficiently different for taxonomic separation only at the subspecies level--the applicable names are *Gulo gulo gulo* (L.) and *G. g. luscus* (L.), respectively; the difference between the fossil (Pleistocene) wolverine of Europe and recent (existing) form of North America was actually less marked than that between the fossil and living forms of Europe, and fossil (late Pleistocene) wolverines of North America are essentially identical to their living descendants; it is hypothesized that *luscus* is a relatively late immigrant, perhaps during the late Illinoian, and that most of the differentiation between the two living subspecies is a result of postglacial evolution.

Liskop, K.S., R.M.S.F. Sadleir, and B.P. Saunders. 1981. Reproduction and harvest of wolverine (*Gulo gulo*) in British Columbia. Pages 469-477 *in* J.A. Chapman and D. Pursley (eds). Worldwide furbearer conference proceedings, Aug. 3-11, 1980, Frostburg, Maryland.

099 A) 1; B) British Columbia; C) Laboratory examination of specimens.
Description - distribution.
Population Dynamics - natality.
Species Management - harvest.
Comments - It is noted that the wolverine originally occupied all of the province except the Queen Charlotte Islands and "the Vancouver area"; the specimen material included 40 females and 44 males collected from trappers in "northwestern B.C." (boundaries and distribution not given) over a 3-year period, 1976-1979; most of the females were apparently young, either 1-year old (n=16), or 2 (n=13); none of the l-year olds was sexually mature, but apparently all but 2 of the 2-year olds and all older animals were; 3 of the older animals, aged 5-7, were judged to be "non-reproductive, showing neither corpora lutea nor placental scars; among the 23 females showing reproductive activity, all of 4 taken in November and December, 4 of 5 in January, 1 of 9 in February and 1 of 5 in March were in a pre-implantation condition; the one exception in January had apparently already given birth, while 5 of 8 in February had uterine embryos and 3 were post-partum, and all the remaining March animals (4) were post-partum; among males, 4 of 14 1-year olds, 7 of 11 2-year olds, and all of the older animals were considered mature; some signs of early spermatogenesis (January - March) were found in 3 males; provincial harvests averaged 200-300 animals from about 1920 through the mid-1960's, then increased to 5-year averages of about 400 by the mid- to late 1970's; it is implied that increased harvests might be related to increasing pelt prices since the mid-1960's, although the stated conclusion is that the harvest increase, particularly in the 1970's, "...is probably due to increased accessibility."

Long, C.D. 1987. Intraspecific communication of the wolverine. Page 13 (abstract only) *in* Townsend, B. (ed). Abstracts of the Fourth Northern Furbearer Conference, 3-4 April 1987, Alaska Dept. Fish and Game, Juneau, Alaska.

100 A) 1; B) General; C) Observation of captive specimens.
Life History - socbehav, behavior.
Comments - Observations designed to "...ascertain the species' methods and mechanisms of communication" were carried out during 679 diel activity periods of captive animals (4 males, 5 females); it is concluded that scent marking by urination is the primary method of communication--comprising 79% and 87% of all scent marking occurrences recorded for males and females, respectively; abdominal rubbing was second (17% and <1%); all occurrences of anal musking were "trauma induced", indicating it is primarily a fear/defense mechanism; two kinds of vocalizations were described, "chuckling" and "growling".

MacDonald, D.W. 1983. The ecology of carnivore social behavior. Nature 301:379-384.

101 A) 1; B) General; C) Literature review.
Life History - socbehav.
Comments - It is speculated that in "less sociable species" such as the bobcat, short-tailed weasel, and wolverine, where several exclusive female territories may be contained within that of one male, female spatial organization may be determined by the distribution of food resources while that of the males is determined primarily by the distribution of females--under the general subject of carnivore social behavior, this pattern is labelled "females as a resource".

MacIver, A.F. 1952. Devil of the north. The Beaver 283 (autumn):22-24.

102 A) 0; B) Northwest Territories; C) Compilation of anecdotes.
Life History - behavior.
Comments - An entertaining account of trapline experiences, focussing on wolverine depredations and interactions with trappers; "To both trapper and public, real interest in the wolverine is not in its name, its appearance, or the value of its pelt, but centres around its behavior characteristics, some sagacious, some diabolic."

Magoun, A.J. 1985. Population characteristics, ecology, and management of wolverines in northwestern Alaska. Unpubl. PhD Thesis, Univ. Alaska, Fairbanks. 197pp.

103 A) 3; B) Alaska; C) Field studies, including telemetry, 1978-81.
Description - features.
Habitat Characteristics - study/area, vegetation.
Life History - food, hmrange, movements, dispersal, socbehav, behavior, health, denning.
Population Dynamics - natality, mortality, poptrend, popcomp, popreg.
Species Management - repro, harvest, harv/strategy.
Comments - The study area was north of the treeline, in arctic tundra, where a wind chill factor of -31° C occurs 50% of the time from December through February; absence of vegetative cover facilitated regular observation of the wolverines; caribou are abundant in the area in summer, but there are no large ungulates present in winter; **AGE DETERMINATION** - a variety of features were evaluated to assign field age, including tooth wear and length of teats or testes; annuli in dental cementum are believed to correspond to age in years; **FEATURES (SIZE)** - average weights for adult males was 14.1 kg (n=7, range 12.5- 15.9) and for females was 9.9 kg (n=12, 9.5-10.9); kits were 55% (males) and 65% (females) of average adult weight by early July (age 4 months), and were within the range of adults by mid-November at 8.5 months (males) and mid-February at 11.5 months (females); a male kit grew 4 mm/day in length and 74 g/day in weight from 12 May to 19 August; **REPRODUCTION** - based on observations of 6 collared adult females over a 5-year period, the "reproductive rate" (kits produced) was 0.69 kits/female/year--adding results for 2 subadults, neither of which produced young, that figure is 0.60 kits/female/year; 1 female averaged 1.25 kits/year over a 4-year period (3

years with kits) while the rate for another was 0.00 kits/year over 3 years of observation; none of 5 collared animals produced young in 1980, an apparently hard year; unsuccessful pregnancies and/or early losses of kits were suspected in a few cases; litter size averaged 1.80 kits for all litters and 1.75 kits for those observed after abandonment of the natal den (i.e., age 2 months and older); **MORTALITY** - no natural mortality was documented; no trapping and only minimal hunting occurs in the area, but one collared male was taken locally by a hunter and 2 males (1 a juvenile after dispersal) were killed outside the study area; apparent trap injuries on the feet of 2 animals suggested that they had dispersed into the area from elsewhere; **HOME RANGE** - summer ranges for females averaged 94 km^2 (n=11 female years, 8 individuals: range 38-318 km^2) and yearly ranges were only slightly larger at 103 km^2 (n=10 f-years, 7 indiv., range 53- 232); average home ranges varied from year to year, and females with young had smaller summer ranges (70 km^2, n=3, 56-99) than those without (97 km^2, n=5, 68-178); at least one female made a long-distance excursion (2-day period in May); male summer ranges averaged 626 km^2 (n=4, range 488-898) and yearly ranges were 666 km^2 (n=4, 488-917); the summer and annual ranges for 3 juvenile males were smaller, averaging 49 and 51 km^2, respectively; it is speculated that the density and reproductive condition of females in an area are more important to male home range size than food or habitat; **TERRITORIALITY** - resident females maintained ranges exclusive of other females, except for female offspring in summer--in one case the range of an adult and her female yearling daughter overlapped extensively; one female made "frequent excursions" into the ranges of other females in winter 1980, probably because of "impending starvation"; male ranges overlapped those of females (usually 4-6 of them) and juvenile males, but data were inadequate to determine whether the ranges of males were mutually exclusive; scent-marking, mostly by urine deposits on protruding objects, was conspicuous (e.g., 40 deposits in 20 km of trail) and was done by both sexes; deposition of secretions from ventral and/or anal glands also occurred, by rubbing--and this appeared to be done with greater "excitement" than was the case for urine deposition; **MOVEMENTS** - the average distance between daily locations (ADDL) varied seasonally, yearly, and among individuals, and was shown to underestimate distances actually moved by 33% in monitored cases; ADDL in summer was 4.2 km for females and 12.3 for males (max. = 15.6 and 35.6 km, respectively); the average rate of travel for unpursued animals was 8.6 km/h for males and 4.6 km/h for females (max. = 10.6 and 8.0); ADDL for females with young was less than for those without, owing to the need to return to dens and/or rendezvous sites; adults (both sexes) moved only about 1 km/day when paired during the mating season; data indicated that males were much more active than females in summer, probably to monitor the several local females for breeding condition; **DISPERSAL** - dispersal of juveniles occurred during their first winter, but not all juveniles dispersed; one female was still in her natal area at 28 months (July); one juvenile male was last monitored on its natal range in mid-November, but dispersed between that date and the following March and was trapped 100 km to the south; other documented dispersals included a juvenile male that left between 9 and 11 March, after periodic forays (10 km) away from his mother in the previous 2-3 weeks, and was relocated 60 km south; an eartagged female, believed a yearling marked on the study area in October, was trapped 300 km south the following January; **WEATHER EFFECTS** - one apparently old female repeatedly intruded on other

female ranges, was livetrapped several times in succession, was the only livetrapped animal to eat the bait, and killed and ate one trapped red fox and tried to obtain another, all in the severe winter of 1980--that year was characterized by reproductive failure of all 5 marked females the following spring; **BEHAVIOR** - females and young are in the natal den for a large proportion of time in March and April, but appear to vacate by early May--probably mostly because of snow melt; females appeared to leave dens to hunt mostly during the mid-day hours--this pattern possibly related to ground squirrel activity at that time; females did not move young from dens when disturbed by human observers; after abandonment of the den, kits are periodically moved to a series of rendezvous sites, where the females leave them when they go foraging; by late June kits travel with their mothers, but may be found separate from them increasingly after August; interactions between mother and young occur throughout the first year, and sometimes longer (especially for female young); breeding behavior was observed (see Magoun and Valkenburg 1983); **FOOD HABITS** - most data are presented in Magoun (1987); caching behavior was conspicuous, with wolverines burying ptarmigan, ground squirrel, and caribou remains in summer, and with frequent evidence of digging out caches in winter; some of the caches utilized by wolverines were believed to have been made by other species, particularly red foxes (whose tracks wolverines regularly followed) and grizzly bears; berries and insects, used in summer in other areas, were uncommon and rarely used in this tundra study area; **DENNING** - detailed diagrams of the extensive snow tunnel systems dug and used as dens are presented; **HARVEST CHARACTERISTICS** - males dominated the harvest in northwestern Alaska, but most harvest was during the denning season (when females were frequently in dens and therefore less vulnerable) and was by shooting rather than trapping; it is suggested that because male ranges are larger, there are fewer of them therefore males are likely to remain transients (with greater vulnerability) longer than females; **MANAGEMENT CONSIDERATIONS** - the most important factor acting on wolverine populations in the area is thought to be food abundance, with particular reference to caribou whose distribution and abundance in the area varies from year to year; a conservative estimate of 821 animals (1 per 48 km^2) is calculated for the foothills region of GMU 26A (1 per 139 km^2 if the adjacent coastal plain area is included); based on known harvests and theoretical considerations of natality and survival observed during the study, it is concluded that the populations in the area were not being overexploited; a skull collection program to ascertain harvest age and sex ratios is recommended as a minimum (and efficient) harvest monitoring activity.

Magoun, A.J. 1987. Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. Can. Field-Nat. 101:392-397.

104 A) 3; B) Alaska; C) Field and laboratory studies.
Life History - food, behavior, health.
Population Dynamics - natality.
Species Management - popreg.
Comments - The study was conducted north of the treeline, where no ungulate wintering occurs; the summer diet, as determined by direct observation of feeding behavior

(capturing, carrying, caching, or eating) among radio-collared animals consisted of arctic ground squirrels (19 of 48 observations, 39.6%), caribou (6, 12.5%), other small mammals (6, 12.5%), 1 observation each of marmot and Willow Ptarmigan (2.1%), and 15 unidentified (probably mostly small mammals and/or birds; of 82 scats collected along winter trails, the top 3 items by frequency of occurrence/percentage dry weight were ground squirrel (40/32), caribou (37/35), and other small mammals (lemmings, voles, shrews, 30/6), while birds and/or eggs (11/3) and unidentified food remains (13/3) also occurred; soil was a frequent and occasionally significant component of scats, particularly those from mid-winter, and was believed to be related to use of cached ground squirrels and/or live or dead individuals in hibernacula; a total of 186 wolverine "digs", with 110 of them into soil, were tabulated along about 80 km of winter trails; caribou and ground squirrels accounted for 92% (weight) of scats collected from natal den sites (representing food consumed primarily in March and April), but the percentages differed between years and between individual sites; it is concluded that wolverines are opportunistic in their food habits, their diet reflecting annual and seasonal changes in food availability; the approximate sequence of food availability and use on the study area was as follows: 1) ground squirrels dominated in the diet from late March through early May (when they first emerged from hibernation), 2) small mammals and birds/eggs increased in the diet in May and June as snow exposed the former and the latter commenced local breeding, 3) caribou migrated through and produced young (late May through June)--with some of all ages dying and/or killed by predators at that time and becoming available to wolverines, 4) ground squirrels increasing in vulnerability during emergence and dispersal of young (especially in August), 5) decreased food availability, October through March, with most ground squirrels apparently taken from caches and old caribou kills being used up; it appears that wolverines are able to derive some nourishment from scanty remains, including bone, but while they may be able to survive a lean winter they may not be able to reproduce the following spring--in one such year, 1979-80, all of 5 radio-collared females failed to produce young; one female, in winter 1981-82, left an established home range in apparent response to a food shortage.

Magoun, A.J., and P. Valkenburg. 1983. Breeding behavior of free-ranging wolverines (*Gulo gulo*). Acta Zool. Fenn. 174:175-177.

105 A) 2; B) Alaska; C) Telemetry-aided field observations.
Life History - behavior.
Population Dynamics - natality.
Comments - Three pairs of breeding wolverines, both members known (radio-collared) in two cases and a known female with an unknown male in the third, were observed; breeding pairs were observed together for up to 2.3 days, and the relationship prior to copulation in two cases was characterized by agonistic behavior from the female in response to male advances; copulation dates were 5 and 11 June 1980 and 6 August 1979, the last date extending the known breeding period for the species; 1 female copulated twice in one day, and both bred in consecutive years, whether or not kits were produced in the previous year.

Makridin, V.P. 1964. The distribution and biology of the wolverine in the far north. Zool. Zhurnal 43:1688-1692.

106 A) 1; B) USSR; C) Field observations and laboratory examination of specimens, incidental to aerial predator control activities.
Description - features.
Life History - food, behavior.
Population Dynamics - poptrend.
Species Management - economics, interactions.
Comments - It is noted that despite their wide distribution and an abundance of food resources, wolverines are rare--found much less frequently than wolves "...even though no special extermination measures have been taken against them" and they have "...no natural enemies other than the wolf"; the yield in some of the more productive areas for the species is given as less than 1 pelt per 5000 km^2 during peak times; it is speculated that low population numbers may be due to reproductive factors, including late maturation (age 3?), alternate year or less frequent breeding, and possibly missed breeding because low densities make it difficult for the animals to find each other; the primary habitat for the species in the northern USSR is "forest tundra", and it is noted that when pursued by aircraft wolverines usually try to escape by hiding in the forest or burrowing into the snow; measurements and weights are given for 14 specimens (9M, 5F)--male weights ranged from 12.5-17.0 kg (mean 14.0) and comparable figures for females were 9.0- 10.4 (9.9); 13 of 16 stomachs examined contained reindeer and 5 contained ptarmigan--those are said to be the two most common species in the tundra and forest-tundra habitats in winter; in winter the wolverine "...confines its movements to reindeer pastures or areas where wild deer or elk congregate," and "...frequently follow wolves and pick over remnants of their prey"; wolverines account for considerable losses in the reindeer herding industry and are "the scourge of polar fox trappers", and the concluded statement notes that "...it is essential that bounties be offered for its extermination and that it be eradicated from most of the regions of the Far North."

McFarland, L.Z., V. Heushele, and P. Werner. 1961. Thymic lymphosarcoma in a wolverine. J. Amer. Vet. Med. Assoc. 139:563.

107 A) 0; B) California; C) Necropsy of a captive (zoo) animal.
Life History - health.
Comments - A 12-year old captive female was euthanized "...because of its debilitation, anorexia, and age" and found to contain a tumour on the thymus gland; the relationship, if any, between the tumour and the animal's condition was not noted, and there are no apparent implications for existence in the wild.

Mehrer, C.F. 1976. Gestation period in the wolverine, *Gulo gulo*. J. Mammal. 57:570.

108 A) 1; B) General; C) Observations of captive animals.
Population Dynamics - natality.

Comments - A pair of wolverines in captivity, both from Montana, were observed to breed on 31 May 1972, and the female (at age 10 years) gave birth to one female and two male kits on 26 February 1973 (272 days gestation); a European source is cited as the only other comparable observation--a zoo breeding in the period 17-22 July 1916 resulted in a litter on 17 February 1917 (about 215 days gestation).

Miller, F.L. 1972. Wolverine in Gatineau Park, Quebec. Can. Field-Nat. 86:390.

109 A) 0; B) Quebec; C) Incidental field observation.
Description - distribution.
Comments - A wolverine, apparently following (chasing?) two white-tailed deer, was observed at close range on 25 March 1972; the sighting was within an area where wolverine occurrence must be considered rare.

Morris, R.F. 1948. The land mammals of New Brunswick. J. Mammal. 29:165-176.

110 A) 0; B) New Brunswick; C) Review of literature and anecdotes.
Description - distribution.
Other Topics - history.
Comments - Wolverines were formerly present, but at the "southern limits of their range" and "never very common"; 8 pelts were exported from St. John between 1764-1774, and an 1884 source is quoted as saying that the species was "occasionally met with" 30 years previous; it is concluded that the wolverine "...is apparently an animal that will not tolerate civilization".

Munro, J.A. 1945. Preliminary report on the birds and mammals of Glacier National Park, British Columbia. Can. Field-Nat. 59:175-190.

111 A) 1; B) British Columbia; C) Brief account of species status and behavior from sight records.
Description - distribution.
Life History - behavior.
Population Dynamics - poptrend.
Comments - Wardens report that fresh tracks are seen daily during winter patrols--commonly along the railway tracks in the area; the total local population was estimated at 12 animals, and 1 individual was said to follow a regular travel circuit that took about 2 weeks to complete.

Munro, J.A., and I. McT. Cowan. 1944. Preliminary report on the birds and mammals of Kootenay National Park, British Columbia. Can. Field-Nat. 58:34-51.

112 A) 1; B) British Columbia; C) Account of species status and distribution from sight records.
Description - distribution.

Habitat Characteristics - vegetation.
Comments - Tracks are reportedly seen every winter, from Sinclair Summit (rarely) to the northern limits of the park (common); the "sub-alpine forest biotic area" is listed as the species' primary local habitat.

Munro, W.T., and L. Jackson. 1979. Preliminary mustelid management plan for British Columbia. Unpubl. Rep., B.C. Ministry of Environ., Victoria. 16pp.

113 A) 1; B) British Columbia; C) Literature review.
Population Dynamics - poptrend.
Species Management - harvest, harv/strategy.
Habitat Management - forestry.
Comments - This document is general for all mustelids, but mentions wolverine specifically on a few pages; the provincial population estimate is 5000-8000 animals, with past annual harvests ranging up to 634, but averaging about 400 in 1976 and 1977; more than 65% of the provincial harvest is from the Omineca-Peace and Skeena Regions; the first priority for use is for commercial use of the fur, while non- hunting recreation (observation) is second; the first "management prescription" listed involves protection of "critical habitat", which is believed to be mature conifer forest, although it is acknowledged that more information is needed; large scale clearcut logging is considered an important adverse activity; annual harvests and average pelt prices for the period 1920-1978 are listed in Appendix B.

Murray, B.M., and D.F. Murray. 1969. Notes on mammals in alpine areas of the northern St. Elias Mountains, Yukon Territory and Alaska. Can. Field- Nat. 83:331-338.

114 A) 0; B) Yukon Territory; C) Incidental field observations.
Life History - behavior.
Comments - A wolverine was seen "backing away" from a red fox, and was twice chased by a dog--it showed neither fear nor aggression in those encounters.

Myhre, R. 1967. Jerven. Fauna Org. 20, Hefte 2, 5:51-63.

115 Not seen: In Norwegian, cited as a "very useful" paper by Dagg and Campbell (1974a), with keywords indicating coverage of distribution, behavior, food, reproduction, territoriality, morphology, taxonomy, and economics.

Myhre, R., and S. Myrberget. 1975. Diet of wolverines (*Gulo gulo*) in Norway. J. Mammal. 56:752-757.

116 A) 1; B) Norway; C) Laboratory study of bountied specimens.
Life History - food.
Comments - Among 77 stomachs containing food remains (winter), the top three items by frequency were reindeer (62, 80.5%), small rodents (11, 14.3%), and moose (6, 7.8%) -- cervid remains were somewhat higher in late winter (after 1 February) than earlier;

other prey in the diet included "birds" (6.5%), red fox (3.9%), hare (3.9%), and roe deer (2.6%); there was some evidence that females might prey on small mammals more frequently than males; cubs began to eat solid food at about 7-8 weeks of age.

Myrberget, S. 1968. [The breeding den of the wolverine, *Gulo gulo*]. Fauna (Oslo) 21:108-115.

117 Not seen: In Norwegian, cited as a "very useful" paper by Dagg and Campbell (1974a), with keywords indicating coverage of habitat, behavior, food, and reproduction.

Myrberget, S., B. Groven, and R. Myhre. 1969. [Tracking wolverines, *Gulo gulo*, in the Jotunheim Mountains, south Norway, 1965-68]. Fauna (Oslo) 22:237-252.

118 Not seen: In Norwegian, cited as a "very useful" paper by Dagg and Campbell (1974a), with keywords indicating coverage of morphology, food, reproduction, sex ratio, territoriality, and tracking.

Nead, D.M., J.C. Halfpenny, and S. Bissell. 1984. The status of wolverines in Colorado. Northwest Sci. 58:286-289.

119 A) 0; B) Colorado; C) Literature review, compilation of solicited sight records, and attempts to confirm reports in the field.
Description - distribution.
Population Dynamics - poptrend.
Comments - Evidence gathered in recent years indicate that wolverines still exist in Colorado (at or near the southern limits of their continental distribution), but it is not certain that there is a "viable population" in the state; wolverines have been protected by law in Colorado since 1965, and has been classified as an endangered species in the state since 1973.

Newby, F.E., and J.J. McDougal. 1964. Range extension of the wolverine in Montana. J. Mammal. 45:485-487.

120 A) 1; B) Montana; C) Compilation of specimen and sight records.
Description - distribution.
Population Dynamics - poptrend.
Comments - A total of 17 new records (1957-1962), 10 involving specimens, indicate that the wolverine has continued to expand its range in Montana, mainly into the southwestern portion of the state, after near extinction in about 1920, and a gradual reappearance (mostly in the northwest) beginning in about 1940; many of the recent specimens were males, suggesting that they are the pioneering sex; females with young, indicating successful reproduction, have been reported more frequently in the northwest (e.g., Glacier National Park), where recolonization of Montana is believed to have begun.

Newby, F.E., and P.L. Wright. 1955. Distribution and status of the wolverine in Montana. J. Mammal. 36:248-253.

121 A) 1; B) Montana; C) Analysis of sighting and capture records.
Description - distribution.
Population Dynamics - poptrend.
Species Management - refuges.
Other Topics - history.
Comments - The Montana wolverine population was believed to have declined almost to extinction by the late 1920's, although it is acknowledged that there is little information on abundance for earlier years; records since the late 1930's suggest that the species has again increased, although it is suspected that dispersal from Canada and protected wilderness in Glacier National Park made such an increase possible; it is speculated that there were also indirect benefits to wolverine from closed or limited marten trapping seasons and from reduced fur prices for both marten and lynx in the 1940's and 1950's-- thus reducing trapping activity and incidental catch of wolverines; records for the early 1950's include individuals in isolated ranges away from the "normal" forested mountains habitat of western Montana, and observation of at least one family group and several pairs.

Patterson, J.R., and E.L. Bowhay. 1968. Four recent records of wolverines in Washington. Murrelet 49:12-13.

122 A) 1; B) Washington; C) Compilation of specimen and sight records.
Description - features, distribution.
Comments - Following a hiatus of wolverine records anywhere in the state for over 20 years, 3 animals were killed and another seen in central (1) and southern (3) counties, April 1963, November 1964, and March 1965; all 3 of the kills involved adult males--2 that were weighed were 28 and 29 lbs (12.7 and 13.2 kg), respectively; reference is also made to an unpublished report of an adult male killed in the Cascade Mountains of Oregon in September 1965--the first authentic record for that state since 1912.

Pengelley, L.W. 1951. Recent records of wolverines in Idaho. J. Mammal. 32:224-225.

123 A) 1; B) Idaho; C) Compilation of specimen and sight records.
Description - features, distribution.
Comments - An adult male, captured in October 1949 and weighing 22 lbs (10.0 kg) after 2-3 days in a trap, apparently constitutes the first authentic specimen record for the state; a few historical anecdotes and two recent (1948 and 1949) sight records are also given; all but one of the records (1926) are from the north (panhandle) area.

Philip, C.B. 1938. A parasitological reconnaissance in Alaska with particular reference to varying hares. II. Parasitological data. J. Parasitol. 24:483-488.

124 A) 0; B) Alaska; C) Post-mortem examination.
Life History - health.
Comments - A wolverine examined incidentally was found to have tapeworms (*Taenia twitchelli* Schwartz) in its small intestine, and it also harbored an apparently new species of flea (genus *Oropsylla*); no management or population implications apparent.

Porsild, A.E. 1945. Mammals of the Mackenzie Delta. Can. Field-Nat. 59:4-22.

125 A) 0; B) Northwest Territories; C) Literature review and interviews.
Description - distribution.
Life History - behavior, dispersal.
Comments - Wolverines were scarce, with few taken by trappers in the area (late 1920's and early 1930's)--many imported from elsewhere to satisfy demand of Eskimos, who paid up to $100 per pelt; the animals "...appear to migrate to the delta region from the mountains and from the barren grounds to the east"; the destructiveness of the animal at caches, uninhabited cabins, and traplines is mentioned.

Powell, R.A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. Z. Tierpsychol. 50:153-165.

126 A) 0; B) General; C) Literature review.
Life History - socbehav.
Comments - "The basic mustelid spacing pattern appears to be intrasexual territoriality....documented for least weasels, stoats, and American pine martens...(and) minks, black-footed ferrets, fishers, beech martens and wolverines (may) also exhibit this spacing pattern"; territorial behavior and food supply are believed to be the main factors affecting the maintenance and stability of the spacing pattern.

Prescott, J. 1983. Wolverine, *Gulo gulo*, in Lake St. John area, Quebec. Can. Field-Nat. 97:457-458.

127 A) 0; B) Quebec; C) Incidental field observation.
Description - distribution.
Species Management - harv/strategy.
Comments - A wolverine, seen in June 1982, may be the first seen in Quebec since the report by Miller (1972); the species continues to be rare, particularly south of 52° N. Lat., and has been protected in the province by law since 1981.

Pulliainen, E. 1963. Occurrence and habits of the wolverine (*Gulo gulo*) in Finland. Suomen Riista 16:109-119.

128 Not seen, but findings have been cited in many papers; identified as a "very useful" paper by Dagg and Campbell (1974a), with keywords indicating coverage of distribution, food, numbers, reproduction, sex ratio, and economics.

Pulliainen, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. Ann. Zool. Fenn. 5:338-344.

129 A) 2; B) Finland; C) Interviews with "wolverine (bounty) hunters".
Life History - denning.
Population Dynamics - natality.
Comments - Data were gathered from 31 natal dens; 25 of the dens (81%) were situated in rocky (fell) habitats--10 (32%) in deep ravines, 8 (26%) at timberline on gentle slopes, and 7 (23%) on similar terrain in subalpine or alpine terrain; the remaining 6 dens (19%) were in spruce and pine peat bogs; all but one were under deep snow (1-3 m), at the ends of tunnels up to 30 m in length, and it is postulated that the snow cover is an important component of natal dens primarily because of its insulative value--the single exception among the 31 dens observed was a den under "spruce brush" at the base of a spruce; in most cases the nest itself was at ground level in a snow chamber, although fallen trees often formed the roof of the chamber where they were present; none of 17 dens in northern Lapland were associated with trees (apparently because trees were generally not available), but 8 of 14 in the taiga habitats of northeastern Lapland used tree structures in some way; for 30 ostensibly complete litters, average litter size was 2.4, with the following frequencies: 1 cub - 4 (13%), 2 cubs - 11 (37%), 3 cubs - 13 (43%), and 4 cubs - 2 (7%); the mean for 161 litters, adding results for other fennoscandian countries, was 2.5, with the following frequencies: 1 cub - 5 (3%), 2 cubs - 81 (50%), 3 cubs - 66 (41%), 4 cubs - 9 (6%); an *in utero* litter of 5 fetuses, near term (15 March 1956), is reported; the sex ratio among 39 sexed cubs was 23 males and 16 females (59:41); the parturition period in Finland lasts about 2 months (late January through late March; males were believed to have visited dens in a few instances, but their parental role (if any) was not evident; female wolverines brought food, mostly carrion, from up to 20 km away and daily movements of 30-40 km away from dens were reported; food items were often stored near the den--in one case 2 reindeer, 39 whole ptarmigan, 32 ptarmigan wings, and the head of a hare (the ptarmigan apparently "stolen" from hunters' traps); one female reportedly killed 12 female reindeer in 4 nights.

Pulliainen, E., and O.S. Alfthan. 1967. Two cases of perodactylus in the same litter of wolverine (*Gulo gulo* L.) in Finland. Ann. Zool. Fenn. 5:338-344.

130 A) 0; B) Finland; C) Examination of animals captured from a natal den.
Life History - health.
Habitat Management - other/impacts.

Other Topics - genetics.
Comments - Foreleg deformities in two wolverine cubs were investigated as possible responses to radiation accumulation in the local ecosystem, but it was concluded that endogenous (genetic) factors were more likely.

Pulliainen, E., and P. Ovaskainen. 1975. Territory marking by a wolverine (*Gulo gulo*) in northeastern Lapland. Ann. Zool. Fenn. 12:268-270.

131 A) 1; B) Finland; C) Tracking in snow.
Life History - socbehav, behavior.
Comments - Along 7.5 km of track (fresh snow) made in one night, a wolverine (sex and age unknown) left "marks" on 26 objects, distributed at a mean distance of 290 m apart; most were small conifers on which rime had been removed and the interpretation was that the animal had rubbed its anal glands across them; urination on a dry stick was also documented, and interpreted as a territorial marking behavior; the animal had slept in two places along the trail, once on snow "between a birch and a stone" at the bottom of a ravine and once "...near a tree in a small spruce stand between two fells"; during the evening's activity the animal unsuccessfully pursued 3 reindeer for about 60 m, and followed "...part of (a) wolf's track."

Quick, H.F. 1952. Some characteristics of wolverine fur. J. Mammal. 33:492-493.

132 A) 0; B) General; C) Review and opinion.
Life History - pelage.
Species Management - economics.
Comments - Contrary to popular opinion, frost or rime *will* form on wolverine fur, but unlike the case for many other furs, the rime readily brushes off; however, the demand for wolverine fur by Eskimos is said to be as much for its beauty and rarity as for its frost shedding qualities.

Quick, H.F. 1953a. Occurrence of porcupine quills in carnivorous mammals. J. Mammal. 34:256-259.

133 A) 1; B) British Columbia; C) Examination of trapped specimens.
Life History - food, behavior.
Comments - Over a two-year period, porcupine quills were found in 5 of 17 fishers (29%), 4 of 12 foxes (25%), 2 of 18 lynx (11%), and in less than 5% of martens, mink, and weasels, but there was no incidence of quills in 15 wolverines examined; the author was of the opinion that a larger sample of wolverines would have revealed some use of porcupines, however.

Quick, H.F. 1953b. Wolverine, fisher, and marten studies in a wilderness region. Trans. N. Amer. Wildl. Conf. 18: 513-532.

134 A) 2; B) British Columbia; C) Field observations and collection of specimens on some northern traplines.
Description - distribution.
Habitat Characteristics - cover.
Life History - movements, behavior.
Population Dynamics - poptrend, popcomp.
Species Management - economics, harvest.
Comments - Based on fur sales data, it is concluded that the Fort Nelson study area may be "a center of wolverine population in western Canada"; acknowledging that yield is related to effort, it is believed that trapping intensity is more directly related to population density in this species than in most others because of the animal's destructive nature and because "...market value does not materially affect trapping intensity"; nevertheless, it is noted that fur sales data are minimal because wolverine pelts are often kept by the trapper and/or sold privately at other than normal outlets; of 44 wolverines known to have been trapped in the study area in 1947 and 1948, only 27 (61%) were killed--the remaining 17 escaped, leaving 1 or more toes in the trap and thereby potentially providing for some consideration of total numbers on a "mark and recapture" basis; observation of tracks along trapline trails and reports from trappers indicated that wolverine abundance was about the same in all of three different habitat "zones" in the study area (muskeg, foothill, and mountain--physiographic subdivisions within the general "Taiga Biome"); the density estimate for the 51 200 km^2 study area was about 1 animal per 207 km^2, for a projected total local population of about 250 animals; recorded harvests for the two study years were 15 and 12 (6.0 and 4.8 per cent of the projected population, respectively); of the 27 wolverines known to have been killed in the study area in the two years, 15 were collected (9 males and 6 females)-- male weights ranged up to 25 lbs (11.3 kg), but females were listed at only 12 lbs (5.4 kg); observations indicated that the wolverine is more of a scavenger than a killer, regularly following "...skillful hunters like lynx, wolf and man"; an account of trapline depredations indicates that wolverines caused less damage and loss of furs than wolves in the study years, and probably less than shrews in all years, although there were regular reports of damage to property such as cabins, panniers, dog harnesses and human food caches; the fur value of wolverines taken in the study area amounted to less than 1% of the total fur revenue in the area overall; it is concluded that the species is unimportant in the fur trade owing to its characteristically low density occurrence, relatively low value per pelt, and the fact that the value of its damage may often exceed the revenues from pelt sales.

Ramirez, P.R.Jr., and M.G. Hornocker. 1981. Small mammal populations in different-aged clearcuts in northwestern Montana. J. Mammal. 62:400-403.

135 A) 1; B) Montana; C) Field studies--trapping and snow-tracking.
Life History - food, behavior.
Habitat Management - forestry.

Comments - Red-backed voles were found active around the bases of trees, where snow depth is least, and snow-tracking indicated that various predators including wolverines, coyotes, martens, and weasels hunted those "tree wells"; forest clearcutting reduced habitat for red-backed voles, greatly diminishing populations, but provided increased habitat for some other small mammal species, including ground squirrels.

Rand, A.L. 1945. Mammals of Yukon, Canada. Nat. Mus. Canada, Bull. No. 100. Ottawa. 93pp.

136 A) 1; B) Yukon Territory; C) Review of literature and anecdotes.
Description - features, distribution.
Life History - behavior.
Species Management - harvest, harv/strategy.
Comments - The wolverine is believed to occur throughout the Yukon, where "Its habit of robbing caches and trap-lines, and taking man's sustenance where it is not easily replaced, makes general protection for it out of the question, and it seems to survive in Yukon very well without it"; one trapper reported losing 4 of 7 that had been in traps in one year; harvests ranged from 164 to 610 in the 1920's, and from 154 to 372 in the 1930's (when prices were very low); a specimen from Alaska (adult male) is said to have weighed 36 lbs (16.3 kg).

Rausch, R.A., and A.M. Pearson. 1972. Notes on the wolverine in Alaska and the Yukon Territory. J. Wildl. Manage. 36:249-268.

137 A) 3; B) Alaska, Yukon Territory; C) Laboratory analysis of specimens and some incidental field observations.
Description - features.
Life History - food, health, denning.
Population Dynamics - natality, popcomp.
Species Management - age/tech, repro, harvest, harv/strategy.
Habitat Management - other/impacts, hab/strategy.
Comments - Note: There are numerous mathematical errors in this paper, especially in Table 5, and the reader is cautioned to check reported numbers before using them--most of the data reported in the present review have been checked and/or recalculated, as appropriate, although some errors may still remain; **FEATURES (SIZE)** - the whole weights of six males averaged 32 lbs., with a range of 29-37 (14.5 kg, 13.2-16.8), while the weights of two females were 21 and 22 lbs (9.5 and 10.0 kg); the projected live weight for one Alaskan male, examined as a skinned carcass, was 42.5 lbs (19.3 kg)--the heaviest wolverine reported; in a sample of 99 whole wolverines from the Yukon, the weights (means and ranges), and sample sizes by age class were as follows:

Males

adults - 31.2, 26.2-36.3 lbs (14.2, 11.9-16.5 kg), n=52
kits - 29.1, 20.7-37.2 lbs (13.2, 9.4-16.9 kg), n=19

Females

adults - 20.7, 18.4-23.7 lbs (9.4, 8.3-10.8 kg), n=21
kits - 20.1, 18.0-22.6 lbs (9.1, 8.2-10.3 kg), n= 7

REPRODUCTION - based on cementum age determinations, none of 109 female wolverines in age class 0 (0-15 months old) were pregnant, while 20 of 40 (50%) in age class 1 (16-28 months) and 90 of 98 (92%) in age classes 2-13 (29 months plus) were; breeding apparently occurs primarily in May through July, implantation in December through March, and most parturition in February and March; males were sexually inactive in late fall and winter, but testis size increased and spermatogenesis began to occur in late winter, peaking in about late May and June; as with females, some (but not all) males were sexually mature by the breeding season of their second year; *in utero* litter sizes of 1-6 were documented, with an average of 3.5 per litter (n=54); among the sample years (1961-68), mean litter sizes of less than 3 were recorded in two (1962 - 2.6, n=5; 1965 - 2.7, n=7), while in 1966 a sample of 5 included four litters of 5 and one of 6 (mean=5.2); **DENNING** - of three natal dens observed in Alaska, two were above timberline in snow-filled ravines and one was in an abandoned beaver house; well-used moose carcasses were present near the two ravine sites; **AGE DETERMINATION AND HARVEST COMPOSITION** - young wolverines grow and develop quickly, reaching adult size by November or December of the first year (age 9-11 months); rapid development of skeletal features reduces options for distinguishing between young and adults--dental cementum is considered the most reliable (although known-aged specimens are still required); males outnumbered females in the trapped samples, but only by 128:100 among kits (age class 0) as compared to 200:100, 450:100, and 178:100 in age classes 1-3, respectively--the ratio among older animals (age classes 5- 12 combined) was 100:100; the even sex ratio among kits is speculated to result from the fact that they had not yet established territories and the sexes were still equally trappable at that age, while the preponderance of young males in the age 1-3 classes is due to greater mobility of males and the even ratio among older animals "...may reflect a reduction of males through exploitation"; **CONDITION** - Kidney fat indices indicated that animals were in the best physiological condition in spring (March-April) and poorest in summer (May-September)--it is speculated that spring is the period of highest food availability for wolverines, especially in terms of ungulate carrion, and that the reproductive cycle is timed to take advantage of that; **FOOD HABITS** - in 94 stomachs containing food and/or trap debris, the top three food items by frequency of occurrence were moose (27 occurrences = 29%), snowshoe hare (23, 24%), and caribou (17, 18%)--other foods included microtines (9%), unident. flesh (6%), bird (3%), fish (3%), beaver (2%), and traces of lynx--the large mammals were believed to have been taken mostly as carrion; it is noted that the wolverine's summer food habits are not well known, but that microtines, ground squirrels, and marmots are taken, and that berries may be heavily used--the stomach of a Yukon specimen shot in September contained 190 g of

blueberries; two instances of internal damage from porcupine quills are reported; **MANAGEMENT** - the wolverine was subject to bounty in Alaska, 1953-1968, but is now classified as a furbearer and big game species; Alaskan harvests have fluctuated considerably over the years (from 300 or fewer to almost 700 animals in the 1950's and 1960's)--the variation is probably mostly related to the general level of trapping activity (e.g. high harvests in the 1960's when lynx were abundant and bringing good prices); management actions believed favorable to wolverines in Alaska, in addition to removal of the bounty, have been outlawing of aerial hunting for the species and termination/reduction of poison baiting aimed at wolves; in regard to poisoning, it is noted that wolverines, "...because of their proclivity for carrion, were particularly susceptible to those nonselective control techniques"; the wolverine is classified as predator and furbearer in the Yukon, with the annual kill attributable to all sources including predator control baiting averaging about 150 animals, but apparently decreasing due both to recently reduced use of strychnine and decreased trapping activity; habitat changes are not considered a threat in Alaska and the Yukon, but garbage and firearm control at remote exploration camps is recommended to minimize detrimental effects on local wolverines.

Rausch, R.L. 1953. On the status of some arctic mammals. Arctic 6:91-148.

138 A) 0; B) Alaska; C) Examination of specimens.
Description - features, taxonomy.
Population Dynamics - poptrend.
Species Management - economics.
Comments - The wolverine section is mainly consideration of the taxonomic status of the species, and includes a table of cranial measurements for 41 specimens; reference is made to pending legislation to provide for a bounty on Alaskan wolverines, and the statement is made that there could be no biological justification for such a law.

Rausch, R.L. 1959. Studies on the helminth fauna of Alaska. XXXVI. Parasites of the wolverine, *Gulo gulo* L., with observations on the biology of *Taenia twitchelli* Schwartz, 1924. J. Parasitol. 45:465-484.

139 A) 1; B) Alaska; C) Post-mortem examination of 80 specimens obtained from trappers and hunters.
Life History - food, health.
Comments - Helminths were found in 69 (86%) of the 80 wolverines examined, as follows: Cestodes - *Mesocestoides kirbyi* (minor infestations in two specimens, i.e., 2.5%), *Taenia twitchelli* (found in 60 wolverines (75%), up to 60 worms per occurrence); Nematodes - *Trichinella spiralis* (found in 19 of 39 specimens (49%) appropriately examined), *Molineus patens* (found in the small intestine of one wolverine, i.e., 1%), *Ascaris devosi* (found in 17 (21%) of the wolverines examined); *Physaloptera torquata* (found in 4 (5%) of the specimens, all from the Brooks Range); in addition, a trematode (*Alaria* sp.) was found incidentally in a captive specimen, and literature reports of occurrence of the nematode *Soboliphyme baturini* are given for single specimens from "Canada" and Montana; winter

food items found incidentally in 20 stomachs during the investigations included moose or caribou (assumed carrion) in 12 (60%), porcupine in 3 (15%), and smaller frequencies for snowshoe hare, red-backed vole, magpie, unident. hawk, unident. bird, and unident. fish--a young animal taken in summer (July) had a vole (*Microtus* sp.) and a ground squirrel in its stomach; life cycle experiments with *Taenia twitchelli* led to the conclusion that the porcupine is the essential intermediate host, and that the wolverine is the primary host; a pers. comm. record from I. McT. Cowan indicates the above parasite was also recovered from a wolverine in the Jasper National Park area, suggesting the two may occur together throughout the wolverine's North American range.

Ritcey, R.W., and R.Y. Edwards. 1958. Parasites and diseases of the Wells Gray moose herd. J. Mammal. 39:139-145.

140 A) 1; B) British Columbia; C) Examination of specimens.
Description - distribution.
Life History - health.
Population Dynamics - poptrend.
Comments - In the range of the Wells Gray moose herd, billed as one of the most productive of the species in the province, wolverines are among the smaller carnivores listed as occurring in "good populations" and is listed as a "suspected host" of adult *Echinococcus granulosus*.

Rust, H.J. 1946. Mammals of northern Idaho. J. Mammal. 27:308-327.

141 A) 0; B) Idaho; C) Review of literature and anecdotes.
Description - distribution.
Life History - behavior.
Comments - Wolverines were formerly present in moderate numbers in the mountains of central Idaho, but little known (present) in the north; records through the 1930's include a report from one trapper who saw one "off and on" over a 6-year period (1931-37), where it followed his trapline.

Ruth, F.S. 1954. Wolverine seen in Squaw Valley, California. J. Mammal. 35:594-595.

142 A) 1; B) California; C) Incidental sighting, 22 July 1953.
Description - distribution.
Life History - food, behavior.
Comments - A wolverine was seen walking about in a meadow occupied by "..an extensive yellow-bellied marmot...colony"; the animal fled to an area of large boulders on a nearby glacial moraine when it became aware of the observers; a scat believed to have been left by the wolverine contained the hair and claws of a ground squirrel (believed to be *Citellus beldingi*).

Scheffer, V.B. 1938. Notes on wolverine and fisher in the state of Washington. Murrelet 19:8-10.

143 A) 1; B) Washington; C) Compilation of sightings and capture records.
Description - distribution.
Population Dynamics - poptrend.
Comments - Estimates for Forest Service districts of 6 animals at Mount Baker, 4 at Snoqualmie, and 10 at Wenatchee are given for 1937; nevertheless, the conclusion is that most wolverines in the state are "...occasional individuals wandering down from Canada"; one observer reported following tracks of one individual for two days--from the headwaters of Ashnola Creek to the International Boundary--without overtaking the animal.

Scheffer, V.B. 1941. Wolverine captured in Okanogan County, Washington. Murrelet 22:37.

144 A) 1; B) Washington; C) Report of an animal killed, 22 March 1941.
Description - features, distribution.
Comments - A large male wolverine, reportedly weighing 40 lbs (18.1 kg), was caught in a coyote trap in "unusual habitat...the center of the Okanogan Valley in Arid Transition terrain at an elevation of 900-1000 feet" (275-300 m).

Schorger, A.W. 1939. Wolverine in Michigan. J. Mammal. 20:503.

145 A) 0; B) Michigan; C) Literature review.
Description - distribution.
Other Topics - history.
Comments - A newspaper report (1860) of a trapped wolverine is cited as the only record of the species for the state.

Schorger, A.W. 1946. Records of wolverine for Wisconsin and Minnesota. J. Mammal. 27:90.

146 A) 0; B) Wisconsin; C) Literature review and compilation of anecdotes.
Description - distribution.
Other Topics - history.
Comments - Records of wolverines seen or killed in 1837 and 1855-56 appear to be applicable to Wisconsin, but no other records are known.

Schorger, A.W. 1948. Further records of the wolverine for Wisconsin and Michigan. J. Mammal. 29:295.

147 A) 0; B) Wisconsin, Michigan; C) Literature review.
Description - distribution.
Other Topics - history.
Comments - Specimen records from 1870 and 1876 indicate that wolverines "...ranged into the southern half of the state"; an anecdote from a trapper's memoirs is used to document occurrence of a wolverine in Michigan in the 1880's.

Scotter, G.W. 1964. Occurrence of a wolverine in southwestern Alberta. J. Mammal. 45:629.

148 A) 0; B) Alberta; C) Report of a road kill.
Description - features, distribution.
Comments - A "barren female" weighing 19.5 lbs (8.8 kg) and apparently in good condition, was run over by a vehicle near Cardston--on the prairie 56 km east of the nearest mountain range; this is the southernmost record for Alberta.

Seton, E.T. 1931. Two records for New Mexico. J. Mammal. 12:166.

149 A) 0; B) New Mexico; C) Anecdotal information.
Description - distribution.
Comments - Based on a report from an Indian, who alleged that wolverines were formerly present in the vicinity of Sante Fe, but "...none of the present generation had seen one...", the primitive range of the species is extended "considerably to the southward".

Sheldon, W.G. 1932. Mammals collected or observed in the vicinity of Laurier Pass, British Columbia. J. Mammal. 13:196-203.

150 A) 1; B) British Columbia; C) Compilation of sight and specimen records.
Description - distribution.
Comments - Wolverine listed as "present", but no useful details.

Shelford, V.E., and S. Olson. 1935. Sere, climax and influent animals with special reference to the transcontinental coniferous forest of North America. Ecology 16:375-402.

151 A) 1; B) North America; C) Review of animal distributions.
Description - distribution.
Habitat Characteristics - vegetation, cover.
Habitat Management - fire, forestry.
Comments - In consideration of animals as indicators of forest associations within the coniferous forest biome of northern North America, the wolverine is considered a "major permeant influent", occurring in climax and various subclimax associations of all three major subdivisions--the pine-hemlock association in the Great Lakes Region, the spruce-balsam fir association from the Atlantic west to the Rockies, and the spruce-pine association in the interior valleys of northern British Columbia, the Yukon, and Alaska.

Shilo, R.A., and M.A. Tamarovskaya. 1981. The growth and development of wolverines (*Gulo gulo*) at Novosibirsk Zoo, U.S.S.R. Internatl. Zoo. Yearbook 21:146-147.

152 A) 1; B) USSR; C) Observations of captive animals.
Life History - nutrition.
Comments - Two young wolverines, estimated at 45-50 days old when captured, were measured and weighed at intervals; most growth in length was complete after about 123 days, although weight increases continued past 148 days; replacement of the milk dentition

began with the incisors (first one at about 85 days and last at 125 days)--molars followed soon thereafter, replacement of premolars took place between 128-150 days and canines were cut at 134-135 days, although milk canines were retained for some days afterward; 3 young born in captivity were blind at birth, covered in short, beige-colored fur, toothless, and had tightly shut ear channels--weights at one day were 85-94 g.

Shufeldt, R.W. 1924. The skull of the wolverine (*Gulo luscus*). J. Mammal. 5:189-193.

153 A) 0; B) General; C) Laboratory examination of one specimen.
Description - features.
Other Topics - morphology.
Comments - A detailed description of the skull, concluding that ...every character and part of this skull clearly indicates that, in life, it belonged to a mammal possessing great strength and a ferocious disposition, and one capable of giving a tremendous bite."

Soper, J.D. 1942. Mammals of Wood Buffalo Park, northern Alberta and District of Mackenzie. J. Mammal. 23:129.

154 A) 0; B) Alberta; C) Review of literature and anecdotes.
Description - distribution.
Population Dynamics - poptrend.
Comments - Wolverines are reported as "scarce", but occasional individuals are caught by local trappers.

Soper, J.D. 1944. Mammals of southern Baffin Island, Northwest Territories, Canada. J. Mammal. 25:233.

155 A) 0; B) Northwest Territories; C) Review of literature and anecdotes.
Description - distribution.
Life History - dispersal.
Comments - Wolverines are considered "rare"; it is speculated that occasional individuals cross the strait from the Melville Peninsula.

Soper, J.D. 1947. Observations on mammals and birds in the Rocky Mountains of Alberta. Can. Field-Nat. 61:148.

156 A) 0; B) Alberta; C) Review of literature and anecdotes.
Description - distribution.
Comments - Wolverines are rare--only occasional appearances in the area.

Soper, J.D. 1948. Mammal notes from the Grande Prairie Peace River region, Alberta. J. Mammal. 29:56.

157 A) 0; B) Alberta; C) Review of literature and anecdotes.
Description - distribution.
Comments - If wolverines are still present in the area, they are rare.

Soper, J.D. 1961. The mammals of Manitoba. Can. Field-Nat. 75:207.

158 A) 0; B) Manitoba; C) Review of literature and anecdotes.
Description - distribution.
Comments - Wolverines are rare--mostly gone from the province by the turn of century.

Soper, J.D. 1973. The mammals of Waterton Lakes National Park Alberta. Can. Wildl. Serv. Rep. Ser. No. 23, Ottawa. 55pp.

159 A) 1; B) Alberta; C) Review of literature and anecdotes.
Description - distribution.
Habitat Characteristics - vegetation.
Comments - Wolverines are "...far from plentiful, widely scattered, and rarely sighted"; the author doubts that they were consistently abundant anywhere in the Cordillera; their habitat is given as "...light to heavily timbered tracts in the Canadian and Hudsonian Zones to the Arctic-Alpine tundras....vertical range extends capriciously from the lowest valleys up to 8000 ft."

Stains, H.J. 1979. Primeness in North American furbearers. Wildl. Soc. Bull. 7:120-124.

160 A) 2; B) North America; C) Review of literature and consultation with professional fur graders.
Life History - pelage.
Species Management - economics, harv/strategy.
Comments - Wolverines are generally prime from the beginning of December through the end of February, but are most prime in December and January.

Stanwell-Fletcher, J.F., and T.C. Stanwell-Fletcher. 1943. Some accounts of the flora and fauna of the Driftwood Valley Region of north central British Columbia. B.C. Prov. Mus. Occas. Pap. No.4. 97pp.

161 A) 1; British Columbia; C) Incidental field observations and anecdotes.
Description - distribution.
Population Dynamics - mortality, poptrend.
Comments - Wolverines were considered rare in the vicinity of Bear Lake, but fairly common farther north (e.g., Tatlatui and Thutade Lakes area); a wolverine and moose skeleton were found together, and it was speculated that they might have killed each other--wolves were not believed to have been involved because the moose skeleton, in particular, was not scattered.

Stephenson, R.O. 1984. The relationship of fire history to furbearer populations and harvest. Alaska Dep. Fish and Game, Unpubl. P-R Prog. Rep., W-22-2, Job 7.13 R, Juneau. 86pp.

162 A) 2; B) Alaska; C) Interviews, mostly with trappers.
Habitat Characteristics - vegetation.

Population Dynamics - poptrend.
Habitat Management - fire.
Comments - The effect of extensive wildfire on wolverines is not clear, but the general consensus appears to be that there is no obvious detrimental effect; wolverines were seen to traverse large, open burns, but didn't use that habitat any more than they used adjacent unburned habitat; as for wolves, "...to the extent that fires benefit moose and other potential prey (including small mammals, snowshoe hares, and beaver) and diversify habitat, they are beneficial..."

Sullivan, T.P. 1986. Influence of wolverine (*Gulo gulo*) odor on feeding behavior of snowshoe hares (*Lepus americanus*). J. Mammal. 67:385-388.

163 A) 1; B) British Columbia; C) Field and captive experiments.
Life History - behavior.
Species Management - interactions.
Comments - Hare live-traps plundered by a wolverine were avoided by hares some time thereafter; subsequent tests showed that hares avoided feeding on young pines "marked" with wolverine urine and were marginally repelled by wolverine anal gland secretion, but were not repelled from feeding on conifers marked with wolverine fecal odor, hare blood, or deer urine; reference is made to similar suppression of feeding by black-tailed deer in response to wolverine urine; it is speculated that "...a predator-prey relationship has evolved whereby both hares and deer (and perhaps other prey species) would presumably choose to avoid an area that was freshly marked by a wolverine rather than risk being preyed upon...strength of response of the prey may be directly related to the initial concentration and age of the scent mark."

Svihla, R.D. 1931. Mammals of the Uinta Mountain region. J. Mammal. 12:256-266.

164 A) 0; B) Utah; C) Historical reports (literature review).
Description - distribution.
Comments - Reports from geological surveyors (1860's and 1870's) indicates that wolverines were formerly present (no recent records).

Swales, W.E. 1938. *Skrjabingylus nasicola* (Leuckart, 1842) Petrow, 1927, a nematode parasitic in the frontal sinuses of American Mustelidae. Livr. Jubv. Prof. Travassos 3:455-459.

165 A) 1; B) Canada; C) Examination of museum specimens.
Life History - health.
Comments - Although the parasite is common in mustelids, none of 19 wolverine skulls in the National Museum showed any evidence of sinus worm infection.

Toner, G.C. 1946. Notes on the mammals of the lower Chilcotin River region, Cariboo District, British Columbia. Can. Field-Nat. 60:87.

166 A) 1; B) British Columbia; C) Compilation of specimen and sight records.

Description - distribution.
Other Topics - history.
Comments - The species was said to have been present prior to 1910, but informants have no recollection of any taken in the past 30 years.

Ulke, T. 1923. Occurrence and distribution of mammals in Yoho Park, British Columbia. Can. Field-Nat. 37:62-64.

167 A) 1; B) British Columbia; C) Compilation of specimen and sight records.
Description - distribution.
Comments - The species is described as present within park boundaries, but not common.

Van Zyll de Jong, C.G. 1975. The distribution and abundance of the wolverine (*Gulo gulo*) in Canada. Can. Field-Nat. 89:431-437.

168 A) 2; B) Canada; C) Literature review.
Description - distribution.
Population Dynamics - poptrend.
Species Management - harvest.
Comments - The wolverine's status in Canada is summarized from available fur harvest and anecdotal information; the species is believed to have been less abundant in the east than in the west in pristine times, and has become "quite rare and restricted in distribution" east of the prairies--annual harvests in each of Ontario and Quebec (including Labrador) apparently has not exceeded 25 animals since the early 1920's and has been less than half that in all years since; in Manitoba, single-year harvests of over 150 are indicated for a few years in the early 1920's, but have remained at 25-50 thereafter--the occupied range has shrunk to the north, with the only known "center of abundance" occurring in the northwest corner; harvests up to 100 were reported for Saskatchewan in the early 1920's, but have been less than 25 in all years since, and the species' range in the province is apparently restricted to the extreme north; occurrence in Alberta is mainly in the north and in mountains along its western border--there were harvests of over 200 (up to about 350) in the 1920's, but the take in most years between 1930 and 1965 was less than 25--a slight trend to increase is evident since 1965, with some harvests in the 50-100 range; there has been no known change in distribution in British Columbia, and changes in abundance (as measured by pelt production) have been less there than in any of the other provinces--annual harvests of 200-300 were common from the 1920's through 1940's, fell off to an average of about 150 through the 1950's and early 1960's, but have shown a dramatic increase trend (to 400 plus) thereafter; in the Yukon, the highest recorded harvests were in the early 1930's, with at least 4 years in the 500-600 range, although most years before and since have been 200-300--no historic change in distribution is indicated, and the harvest trend in recent years (1970's) appears to be upward; occasional yearly harvests of 200- 300 are shown for the Northwest Territories in the 1920's and 1930's, but except for peaks of about 150 in the late 1930's and several years in the late 1950's, most years since the 1930's have produced 50-100 pelts--the distribution in NWT has apparently been maintained, but no trend to increasing numbers (as reflected in harvests) is apparent; it is noted that at the time of writing, there had been "...virtually no field studies on this continent", but the animal's

scavenging life style is apparent and that observed changes in Canadian distribution and abundance since the early part of this century are believed related mostly to human predation, changes in ungulate populations (especially caribou), and possibly wolf control.

Webster, J.D. 1949. Notes from southeastern Alaska. J. Mammal. 30:81.

169 A) 1; B) Alaska; C) Incidental field observation.
Description - distribution.
Life History - food.
Comments - Though apparently absent from islands of the Alexander Archipelago, the wolverine is reportedly common on Wrangell Island (just offshore, south of the Stikine River mouth); on 4 May 1946 a wolverine was seen on a beach of that island, eating an American Widgeon.

Whitman, J.S., W.B. Ballard, and C.L. Gardner. 1986. Home range and habitat use by wolverines in southcentral Alaska. J. Wildl. Manage. 50:460-462.

170 A) 2; B) Alaska; C) Field (telemetry) studies, 1980-83.
Habitat Characteristics - cover.
Life History - hmrange, movements.
Comments - Adequate data for home range considerations were obtained for 7 animals (4M,3F); males had significantly larger home ranges (535 km^2) than females (105 km^2), although all females had kits during most of the monitoring period and were therefore probably more sedentary than other females might have been; summer and winter ranges were similar in size, and overlapping--the animals tending to expand the overall annual range by using different areas in the two seasons; animals of both sexes moved to high elevation for summer, where ground squirrels, other small mammals and ground-nesting birds are plentiful, and in winter moved to lower elevations where ungulates dying from starvation and wolf predation were available; in summer, forest habitat types were avoided and other types (shrub, tundra, rock-ice) were used according to their availability; in winter, tundra was avoided and the other types.used according to their availability.

Wilber, C.G. 1946. Mammals of Knik River Valley, Alaska. J. Mammal. 27:213-216.

171 A) 0; B) Alaska; C) Anecdotal information.
Description - distribution.
Life History - behavior.
Comments - Wolverines are listed simply as "present," with anecdotes about depredations on cabins and caches.

Williams, J.F., and A.W. Dade. 1976. *Dirofilaria immitis* infection in a wolverine. J. Parasitol. 62:174-175.

172 A) 0; B) Ontario; C) Necropsy of a captive animal.
Life History - health.

Comments - A male wolverine from Ontario was held in captivity in an outdoor pen for 17 years; at death it was found to have a heavy load of heartworms, which had resulted in severe vascular and pulmonary disease; although it was believed that the worms had been acquired locally, probably from domestic dogs, it was concluded that "...the wolverine could (apparently) contribute to natural transmission of heartworms in enzootic areas, and that its susceptibility is sufficient to permit pathogenic worm burdens to develop.

Wilson, D.E. 1982. Wolverine. Pages 644-652 *in* J.A. Chapman and G.A. Feldhamer (eds). Wild mammals of North America. Biology, management, and economics. Johns Hopkins Univ. Press, Baltimore.

173 A) 1; B) North America; C) Literature review.
Description - features, distribution.
Habitat Characteristics - vegetation.
Life History - lifehist.
Species Management - refuges.
Comments - Intended as a comprehensive review of wolverine biology and management, compilation of this paper predated the earliest intensive field study (Hornocker and Hash 1981) and is therefore limited in scope; because it largely draws from literature described in detail in the present annotated bibliography, it will not be extensively quoted--only new information and/or unique interpretations follow; wolverines are said to be "...especially fond of marshy areas"; they are limited to montane areas in the southern extremities of their range; the status of the species is outlined for several areas of the U.S. (state by state), but there is little mention of Canada; "It is axiomatic that a management plan...should consider the possible effects on other species, such as predators, competitors, and prey items...assuming that the goal of such a plan is to maintain optimum population size...it is possible that the best way to manage this species is to do nothing--wolverines would probably flourish if sufficiently large tracts of proper habitat were set aside and protected"; maintenance of populations in Alaska and Canada are seen as key to the species survival.

Withers, P.C., T.M. Casey, and K.K. Casey. 1979. Allometry of respiratory and hematological parameters of Arctic mammals. Comp. Biochem. Physiol. 64A:343-350.

174 A) 0; B) Alaska; C) Studies of captive animals.
Other Topics - physiology.
Comments - Wolverines were among mammals sampled in these studies, but results for that species were apparently not significant and were not featured in the discussion or summary sections.

Wood, N.A. 1921. A wolverine in a tree. J. Mammal. 2:234.

175 A) 0; B) Wyoming; C) Anecdotal information.
Description - distribution.
Life History - behavior.

Comments - In response to Grinnell's (1920) comments about the tree- climbing abilities of the wolverine, the author calls attention to a photograph of one that had been treed in Wyoming, 1907.

Woods, G.T. 1944. Longevity of captive wolverines. Amer. Midland Nat. 31:505.

176 A) 1; B) General; C) Correspondence with various zoological parks.
Population Dynamics - popcomp.
Comments - Of 45 captive wolverines for which information was received, and which survived at least 6 months, the average length of life was about 5.5 years; the maxima recorded were for 4 animals listed as "close to 16 years old" and one other at 15 years.

Wright, P.L., and R.L. Rausch. 1955. Reproduction in the wolverine, *Gulo gulo*. J. Mammal. 36:346-355.

177 A) 2; B) Alaska; C) Laboratory examination of 33 trapped specimens.
Population Dynamics - natality.
Species Management - age/tech.
Comments - These studies confirmed that delayed implantation occurs in the wolverine--adult females taken in October through mid-January showed unimplanted blastocysts in their uteri and inactive corpora lutea in their ovaries; embryos were found in 2 females, taken 20 January and 2 February, and 2 females taken in April were lactating; implied "litter" sizes were: blastocysts - 2,4,4; embryos - 3,4; placental scars - 3,3; it was concluded that breeding probably occurs in mid-summer, implantation in January, and birth in late March or early April; the testes of males were largely inactive in winter, when the specimens were collected--only 1 of 22 (taken in early April) showed signs of full sexual activity; the evidence indicated that sexual maturity was reached by both sexes in the second year; the skull matures rapidly, although the extent of the sagittal crest remains a method of distinguishing between adults and juveniles.

Yocom, C.F. 1973. Wolverine records in the Pacific coastal states and new records for northern California. Calif. Fish Game 59:207-209.

178 A) 0; B) California; C) Literature review and compilation of incidental sight records.
Description - distribution.
Population Dynamics - poptrend.
Comments - A total of 12 sight records between 1958 and 1970, and recent literature reports of animals in Washington and Oregon, are taken to indicate that the species "...may be increasing in abundance in these portions of their ranges since the late 1950's"; in particular, it is believed that wolverines are becoming established in the mountainous areas of northwestern California.

Yocom, C.F. 1974. Recent wolverine records in Washington and Oregon. Murrelet 55:15-18.

179 A) 1; B) Washington, Oregon; C) Compilation of specimen and sight records.

Description - distribution.
Population Dynamics - poptrend.
Comments - Numerous additional sightings, two photographs, and at least one specimen, sex not given but at 33 lbs (15.0 kg) probably a male, documented for period from the mid-1960's through the early 1970's; these records are said to substantiate a previous conclusion that the species has increased in abundance in the two states in recent years; increase from "surviving nuclei" in Washington and Oregon and spread of animals from British Columbia and northwestern Idaho are both considered as contributing to the observed increases.

Youngman, P.M. 1975. Mammals of the Yukon Territory. Natl. Mus. Canada Publ. Zool. No. 10, Ottawa. 192pp.

180 A) 1; B) Yukon Territory; C) Incidental field observations.
Life History - food, behavior.
Comments - Two subadults collected in the Ogilvie Mountains had fur and portions of the feet of hoary marmots in their stomachs; those two animals and one other (apparent littermates) were traveling together in mid-August; dens ("temporary feeding dens") have been seen in alpine tundra habitat "...usually among rocks...all in exposed sites that afforded an excellent view of the surrounding countryside" and all containing "...splintered skeletal remains of such prey as sheep, caribou, and marmots."

* * * * *

SUBJECT INDEX

The following index is organized under the descriptive elements characterizing aspects of the literature assembled (A), and by the subject headings and keywords relating to contents of that literature (B), all as described under "format" (section 3.2). For each topic, the number (N) and frequency of its occurrence (%) among the total papers indexed (T) are given in parentheses. The three digit identification numbers are those preceding the individual bibliographic entries in section 3.3.

A) CHARACTERISTICS OF THE LITERATURE

Geography (T=183): Locations of the observations, studies, and analyses reported.

Holarctic (N=2, 1.1%) - 097, 098.

North America, general (N=5, 2.7%) - 026, 035, 151, 160, 173.

Canada, general (N=7, 3.8%) - 009, 031, 032, 068, 088, 165, 168.

Provinces and Territories (N=54, 29.5%)

Alberta (N=7, 3.8%) - 043, 045, 148, 154, 156, 157, 159.

British Columbia (N=26, 14.2%)
002, 006, 008, 022, 025, 027, 028, 029, 039, 051, 056, 069, 070, 099, 111, 112, 113, 133, 134, 140, 150, 161, 163, 166,167.

Manitoba (N=1, 0.5%) - 158.

New Brunswick (N=1, 0.6%) - 110.

Newfoundland (N=1, 0.6%) - 061.

Northwest Territories (N=10, 5.5%)
001, 028, 031, 039, 086, 087, 109, 171, 207, 252.

Ontario (N=2, 1.1%) - 021, 172.

Quebec (N=2, 1.1%) - 109, 127.

Yukon Territory (N=4, 2.2%) - 007, 114, 136, 180.

United States (N=72, 39.3%)

Alaska (N=25, 13.7%)
003, 004, 019, 022, 033, 038, 061, 074, 079, 085, 093, 161, 172, 180, 183, 206, 225, 229, 231, 261, 268, 269, 271, 275, 278.

California (N=9, 4.9%)
030, 037, 046, 084, 085, 090, 107, 142, 178.

Idaho (N=2, 1.1%) - 123, 141.

Montana (N=8, 4.4%) - 034, 065, 071, 072, 089, 120, 121, 135.

Minnesota (N=5, 2.7%) - 015, 078, 081, 082, 146.

Washington (N=5, 2.7%) - 083, 122, 143, 144, 179.

Wisconsin (N=4, 2.2%) - 079, 080, 146, 147.

Wyoming (N=4, 2.2%) - 067, 073, 074, 175.

(N=1, 0.6%):
Colorado - 119; Iowa - 066; Michigan - 145; Nebraska - 013; Nevada - 011; New Hampshire - 077; New Mexico - 149; Oregon - 145.

Eurasia (N=23, 12.6%)

Country unidentified (N=5, 2.7%) - 014, 060, 091, 092, 093.

Finland (N=6, 3.3%) - 086, 094, 128, 129, 130, 131.

Norway (N=5, 2.7%) - 076, 115, 116, 117, 118.

Sweden (N=3, 1.6%) - 057, 058, 095.

USSR (N=4, 2.2%) - 033, 042, 106, 152.

General--No specific Location (N=20, 10.9%)
005, 018, 020, 038, 040, 041, 052, 053, 055, 059, 062, 064, 075, 100, 101, 108, 126, 132, 153, 176.

Management Significance (T=175): Papers were subjectively rated as having high, medium, low, or nil significance in terms of implications for management; only the highs and mediums are listed below.

High (N=7, 4.0%)
007, 047, 071, 095, 103, 104, 137.

Medium (N=20, 11.4%)
004, 005, 006, 016, 032, 048, 057, 064, 068, 072, 088, 089, 105, 129, 134, 160, 162, 168, 170, 177.

Primary Study Methods (T=175):

Field (outdoor) Studies (N=66, 37.7%)

Telemetry (N=5, 2.9%) - 007, 047, 071, 103, 170.

Snow-tracking (N=6, 3.4%) - 025, 042, 057, 089, 131, 135.

Multi (several methods, N=2, 1.1%) - 095, 104.

Incidental Observations (N=51, 29.1%)
011, 014, 016, 019, 022, 024, 030, 043, 045, 046, 048, 049, 050, 054, 055, 056, 063, 066, 067, 069, 073, 078, 081, 085, 087, 091, 096, 102, 105, 106, 109, 111, 112, 114, 120, 122, 123, 127, 140, 142, 143, 144, 148, 150, 161, 166, 167, 169, 175, 179, 180.

Other (drug testing, etc. N=3, 1.71%) - 005, 114, 163.

Laboratory Studies (Autopsy and analysis of harvest samples and scats, study of museum specimens, observations and experiments with captive specimens, N=35, 20.0%)
001, 020, 023, 033, 034, 044, 051, 052, 059, 060, 062, 075, 076, 079, 086, 097, 098, 099, 100, 107, 108, 116, 124, 130, 133, 134, 137, 138, 139, 152, 153, 165, 172, 174, 177.

Indoor (Paper) Studies (N=73, 41.7%)

Review, Synthesis, Anecdote papers (N=64, 36.6%)
002, 003, 006, 009, 012, 013, 015, 017, 018, 021, 026, 027, 028, 029, 032, 035, 036, 040, 041, 053, 058, 061, 064, 068, 070, 072, 074, 077, 080, 082, 083, 084, 088, 090, 092, 094, 101, 110, 113, 119, 121, 125, 126, 132, 136, 141, 145, 146, 147, 149, 151, 154, 155, 156, 157, 158, 159, 160, 164, 168, 171, 173, 176, 178.

Harvest Data Analysis (N=4, 2.3%) - 008, 010, 037, 039.

Bibliography (N=3, 1.7%) - 005, 031, 038.

Interview (N=2, 1.1%) - 129, 162.

B) BIOLOGY AND MANAGEMENT OF THE LYNX: SUBJECT HEADINGS AND KEYWORDS (T=175)

Description (N=92, 52.6%): Aspects of the physical and geographical identity of the species.

Features (N=23, 13.1%)
007, 009, 026, 027, 029, 041, 047, 051, 064, 065, 066, 087, 103, 106, 122, 123, 136, 137, 138, 144, 148, 153, 173.

Taxonomy (N=9, 5.1%)
006, 026, 027, 051, 064, 088, 097, 098, 138.

Distribution (N=84, 48.0%)
006, 007, 008, 009, 011, 012, 013, 015, 021, 022, 024, 026, 027, 029, 030, 032, 035, 036, 039, 049, 061, 063, 064, 066, 067, 068, 073, 074, 077, 078, 079, 080, 081, 082, 083, 084, 085, 087, 088, 090, 092, 099, 109, 110, 111, 112, 119, 120, 121, 122, 123, 125, 127, 134, 136, 140, 141, 142, 143, 144, 145, 146, 147, 148, 149,150, 151, 154, 155, 156, 157, 158, 159, 161, 164, 166, 167, 168, 169, 171, 173, 175, 178, 179.

Habitat Characteristics (N=19, 10.9%):

Study/Area (N=3, 1.7%) - 007, 071, 103.

Vegetation (N=12, 6.9%)
029, 039, 040, 057, 064, 092, 103, 112, 151, 159, 162, 173.

Cover (N=9, 5.1%)
007, 047, 064, 071, 094, 095, 134, 151, 170.

Climate (N=2, 1.1%) - 007, 095.

Life History (N=89, 50.9%)

Lifehist (General coverage, N=8, 4.6%)
009, 026, 029, 064, 068, 080, 088, 173.

Food (N=28, 16.0%)
007, 012, 016, 019, 041, 046, 047, 050, 056, 057, 058, 066, 071, 073, 074, 086, 095, 103, 104, 106, 116, 133, 135, 137, 139, 142,169, 180.

Nutrition (N=6, 3.4%)
034, 040, 043, 044, 076, 152.

Activity (N=3, 1.7%) - 044, 057, 095.

Hmrange (Home Range, N=6, 3.4%) - 007, 025, 047, 071, 103, 170.

Socbehav (Social Behavior, N=14, 8.0%) - 007, 020, 047, 057, 059, 071, 072, 089, 095, 100, 101, 103, 126, 131.

Movements (N=8, 4.6%) - 007, 025, 047, 057, 071, 103, 134, 170.

Dispersal (N=8, 4.6%) - 007, 047, 048, 071, 072, 103, 125, 155.

Health (N=18, 10.3%)
001, 007, 016, 060, 066, 069, 070, 086, 103, 104, 107, 124, 130, 137, 139, 140, 165, 172.

Denning (N=7, 4.0%) - 041, 057, 064, 094, 103, 129, 137.

Pelage (N=4, 2.3%) - 034, 062, 132, 160.

Behavior (N=46, 26.3%)
007, 012, 016, 019, 034, 040, 041, 043, 045, 046, 047, 049, 050, 052, 053, 054, 055, 056, 057, 058, 063, 071, 091, 094, 095, 096, 100, 102, 103, 104, 105, 106, 111, 114, 125, 131, 133, 134, 135,136, 141, 142, 163, 171, 175, 180.

Population Dynamics (N=58, 33.1%)

Cycles (N=3, 1.7%) - 017, 018, 028.

Natality (N=17, 9.7%)
007, 033, 034, 040, 041, 064, 071, 095, 096, 099, 103, 104, 105, 108, 129, 137, 177.

Mortality (N=9, 5.1%)
007, 016, 019, 047, 050, 064, 071, 103, 161.

Popcomp (Sex and/or age composition, N=8, 4.6%)
007, 032, 043, 071, 103, 134, 137, 176.

Poptrend (Population densities, indices, or status, N=36, 20.6%)
003, 007, 008, 021, 028, 031, 032, 037, 040, 042, 046, 064, 067,068, 071, 081, 083, 084, 088, 103, 106, 111, 113, 119, 120, 121, 134, 138, 140, 143, 154, 161, 162, 168, 178, 179.

Popreg (Population regulation, limiting factors, N=4, 2.3%)
007, 088, 103, 104.

Species Management (N=45, 25.7%)

Census (Techniques, N=1, 0.6%) - 064.

Age/Tech (Age determination techniques, N=5, 2.9%)
006, 007, 047, 137, 177.

Gen/Tech (Field study methods, N=4, 2.3%) - 004, 043, 065, 071.

Kill/Tech (Collecting and analyzing harvest data, N=1, 0.6%) - 007.

Repro (Assessing productivity, N=3, 1.7%) - 007, 103, 137.

Economics (Fur value, depredations, N=12, 6.9%)
024, 042, 050, 057, 058, 064, 068, 106, 132, 134, 138, 160.

Harvest (Nature, extent, and/or effects, N=16, 9.1%) - 003, 007, 008,
010, 028, 031, 037, 039, 047, 099, 103, 113, 134, 136, 137, 168.

Interactions (Relationships with other species, N=12, 6.9%)
007, 016, 019, 050, 053, 055, 056, 057, 092, 095, 106, 163.

Harv/strategy (Harvest options, recommendations, N=15, 8.6%)
002, 007, 010, 032, 037, 064, 068, 071, 088, 103, 113, 127, 136, 137, 160.

Transplants (N=2, 1.1%) - 064, 088.

Refuges (Parks, management areas, N=3, 1.7%) - 071, 088, 173.

Habitat Management (N=10, 5.7%)

Fire (N=3, 1.7%) - 003, 151, 162.

Other/Nat (Effects of other natural forces, N=1, 0.6%) - 086.

Forestry (N=4, 2.3%) - 071, 113, 135, 151.

Other/Impacts (Effects of human developments other than forestry, N=3, 1.7%) - 002,
130, 137.

Hab/strategy (Recommendations, prescriptions, N=3, 1.7%) - 002, 071, 137.

Other Topics (N=30, 17.1%)

History (N=14, 8.0%)	-	014, 021, 028, 032, 064, 068, 078, 083, 110, 121, 145, 146, 147, 166.
Bibliography (N=3, 1.7%)	-	005, 031, 038.
Paleontology (N=3, 1.7%)	-	014, 097, 098.
Zoogeography (N=1, 0.6%)	-	098.
Physiology (N=5, 2.9%)	-	023, 044, 075, 076, 174.
Morphology (N=5, 2.9%)	-	020, 052, 059, 098, 153.
Evolution, Genetics (N=3, 1.7%)	-	041, 097, 130.

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Copies of Wildlife Bulletins can be obtained, depending on supply, from the Wildlife Branch, Ministry of Environment, Parliament Buildings, Victoria, B.C. V8V 1X5. Titles of Bulletins 1 to 21 are also available.

No. B-22 Landsat classification for wildlife habitat management and research planning: problem analysis. K.L. Sadoway. December 1980. 36pp. (Also printed as IWIFR-6).

No. B-23 Landsat classification: evaluation of image analysis methodologies for wildlife habitat management and research planning: working plan. K.L. Sadoway. May 1980. 29pp. (Also printed as IWIFR-7).

No. B-24 Landsat classification: evaluation of image analysis methodologies for wildlife habitat management and research planning: final report. K.L. Sadoway, ed. July 1983. 177pp. (Also printed as IWIFR-8).

No. B-25 A bibliography of the wolverine *Gulo gulo*. V. Banci. June 1982. 53pp. (Also printed as IWIFR-9).

No. B-26 Problem analysis: grizzly bears and coastal development, with particular reference to intensive forestry. W.R. Archibald. September 1982. 24pp.

No. B-27 The wolverine in British Columbia: distribution, methods of determining age and status of *Gulo gulo vancouverensis*. V.A. Banci. June 1982. 90pp. (Also printed as IWIFR-15).

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No. B-37 Vancouver Island Roosevelt elk/intensive forestry interactions: progress report 1981-1984. J. Youds, K. Brunt and D. Becker. 1985. (Also printed as IWIFR-21).

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